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Sexual recruitment of trees following fire in the southern mixedwood boreal forest of Canada.

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A Thesis

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ABSTRACT

Sexual recruitment of trees following fire in the southern mixedwood boreal of Canada.

Isabelle Charron

The establishment following fire of four tree species, *Pinus banksiana* Lamb., *Picea mariana* (L.) Mill., *Picea glauca* (Moench) Voss and *Populus tremuloides* Michx., was studied in the mixedwood boreal forest of Saskatchewan, Canada. The main objective of the study was to estimate the recruitment densities of germinants as a function of seedbed type. Field observations indicate that there are significant differences in seedbed frequencies between sites. The study also demonstrates that all species establish preferentially around tree boles where there is exposed mineral soil and humus. While there is no significant difference between germinant densities on mineral soil and humus, there are, on average, two times more germinants on those seedbeds than on organic layer (O_f) seedbeds. In addition, there is evidence for an inverse relationship between germinant survival and organic layer thickness. There is also evidence that moisture is the major factor controlling germinant survival in the field. The study shows that a sequence of stage-specific survival values can be used to accurately estimate recruitment densities. Finally, it demonstrates that there are essentially only three cohorts following a fire; that germinant mortality declines with time; and that survival subsequently approaches one and becomes independent of seedbed type. The results of the study now give investigators a standard for comparison with post-clearcut recruitment densities.

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INTRODUCTION

There is a growing belief among foresters, driven perhaps by environmentalists' arguments, that harvesting regimes in the boreal forest should mimic natural disturbances. However, the processes involved in natural regeneration are not yet understood and so far attempts at naturally regenerating even relatively small clear-cut areas have not been reliably successful. Therefore, it is not clear why and how this goal should be accomplished and thus the program is premature. In order to accurately predict recruitment after a disturbance, we first need to understand natural regeneration processes, i.e. understand sexual and asexual regeneration.

In the boreal forest, at least in the west, the major disturbance is stand-replacing crown fire, where usually less than five percent of the trees survive (Johnson 1992). Disturbances are episodic, their spatial scale exceeds the dispersal capacity of all trees, while their temporal scale is shorter than the typical senescence time of most trees (Johnson 1992). The boreal forest is a species poor system where both coniferous and deciduous tree species have wind-dispersed seeds and reproduce sexually. Although the hardwood species are capable of reproducing asexually, asexual reproduction will not be dealt with in this study. The advanced regeneration and soil seed banks suffer complete mortality during wildfires (Johnson 1992; Black and Bliss 1980). New seedlings must therefore establish from newly dispersed seeds. It has been shown that all species are capable of establishing themselves immediately after a disturbance (St-Pierre *et al.* 1992).

These initial cohorts eventually form the canopy and there is usually insufficient time for the slow replacement of canopy stems by shade-tolerant species in small-gap regimes (Johnson 1992), and thus succession is not believed to play an important role in shaping the community structure of the mixedwood boreal forest system. Thus, the species composition of the stands is essentially determined by the post-fire recruitment episode (St-Pierre *et al.* 1992; Morneau and Payette 1989; Black and Bliss 1980).

The recruitment density after a disturbance is influenced by source strength (the product of seed production per tree and tree density), dispersal capacity, the production of asexual stems and the mortality of sexual stems. Greene and Johnson (1997) have developed a recruitment model for boreal forest tree species that takes into account these factors but their post-fire mortality estimate is a single fraction dependent only on seed mass. Therefore, to accurately predict recruitment densities after a disturbance, we must examine the factors that influence post-fire survival of establishing stems. In particular, as the relative frequencies of seedbed types in natural burns and site prepared cuts are not expected to be similar, a study of the interaction of seedbed characteristics and survival is needed.

Dormancy and germination requirements

The germination requirements of boreal forest species are straightforward. First, all species, except poplars, require an overwintering period in order to germinate (Young and Young 1992). In the spring, available moisture is the most important factor that will allow seeds to germinate (Kozlowski 1971). All seeds can germinate at very low light levels (Young and Young 1992; Kozlwoski 1971). The post-abscission dormancy period of seeds decreases rapidly with time and is almost invariably less than a year, and about two weeks to a month for poplar species (Young and Young 1992; Zazada *et al. In* Shugart *et al.* 1992). The viability of black spruce and jack pine seeds, the two most abundant species, has also been shown to greatly decrease with time-since-fire (Groot 1996; Fleming and Mossa 1996, 1995b; Thomas and Wein 1985b; St-Pierre *et al.* 1992;)

Seed abscission

The seed availability of boreal species, except for jack pine and black spruce, is independent of time-since-fire and highly variable from one year to the next. It is therefore unpredictable on an annual basis. For example, all species show mast years, which are years of very high seed production. As a general rule, three years out of ten will account for about 90% of the seed production in a decade (David Greene, pers. comm.). However, jack pine has serotinous cones, which primarily release their cumulative annual seed production immediately after an intense fire. Likewise, black spruce has semiserotinous cones, where, although the bulk of a seed cohort will abscise a few years after maturation (regardless of whether a fire has occurred), there is a marked increase in abscission following a fire (Zazada *et al. In* Shugart *et al.* 1992). Studies on the depletion of the aerial seed banks of jack pine and black spruce show that most seeds are released within the first three years following a fire or a clearcut (Fleming and Mossa 1995a; Fleming and Mossa 1994; St-Pierre *et al.* 1992; Black and Bliss 1980).

Seedbed type

Disturbances such as fires greatly affect the environment in which the germinants must establish. The removal of the canopy and understory stems first alters the amount of light reaching the ground which will in turn affect the temperature and water holding capacity of the soil. The distributions and proportions of the different seedbeds also change after a fire, the major changes being an increase in exposed mineral soil and humus and a decrease in the thickness of the remaining duff (a term used by foresters that includes all organic layers) (Dyrness and Norum 1983; Chrosciewicz 1976).

There are three major types of seedbeds present following a fire. The first seedbed is mineral soil. The second type is the humus layer, the O_H layer, which is the most highly decomposed part of the organic layer (Clayton *et al.* 1977). It has the least amount of fiber, has the highest bulk density and the lowest saturated water-holding capacity of the organic substrates (Clayton *et al.* 1977). The third seedbed is the O_f layer, which will also be referred to as the organic layer seedbed in this paper. This porous, fibric layer has a large quantity of identifiable fibers and is the least decomposed of all the organic soil materials (Clayton *et al.* 1977). Litter, such as leaf litter, is removed by fires but may quickly accumulate on favourables seedbeds. Although burned needles fall to the forest floor after fires, they do not usually form thick layers (pers. obs.). Subsequently, pioneer mosses, liverworts and different perennials will also invade the sites.

First-year mortality and water availability

There are many different causes of first-year mortality. Some of them such as granivory, herbivory and fungal infection will not be dealt with in this paper. Many studies argue that the two most important causes of germinant mortality are heat injury and drought (Cayford 1963; Day 1963; Smith 1951). Heat injury is often difficult to account for as it affects mostly the youngest germinants which rapidly dessicate and become invisible to the observer. Drought affects older germinants and is a more readily observable cause of mortality. I only concentrate on causes of mortality related to water-availability (i.e. drought). Water affects juvenile mortality in two ways. First, water availability must be sufficient for seeds to germinate (Kozlowski 1971). Second, subsequent water content must remain high enough to prevent the seedbeds from drying up, which would kill the germinants. There are two factors that influence water availability during germination. The first one is related to annual precipitation. Drought years will obviously be less favourable for germination than years of ample precipitation, but clearly the effects will be more dramatic on high porosity seedbeds such as organic layers. However, annual precipitation cannot be predicted at present. The nature of the seedbeds is the second factor that affects water availability during germination. Of the three seedbed types present after a fire, mineral soil is undoubtably the best for germination and survival (Fleming and Mossa 1995a; Day 1964; Day and Duffy 1963; Day 1963), although mortality from heat injury may occur on coarser, dryer mineral soil that has a lower conductivity (Smith 1951). Mineral soil shows smaller fluctuations in humidity and temperature because it can rapidly conduct heat from the surface downwards (Duchesne and Sirois 1995; St-Pierre *et al.* 1991; Day 1963; Smith 1951). High specific heat and high conductivity, such as that of mineral soil, will positively affect the water availability of a seedbed. Therefore, mineral soil usually has a relatively high water content (Duchesne and Sirois 1995; St-Pierre *et al.* 1991). On the other hand, the organic layer (O_f layer) is a better insulator and therefore does not conduct heat as well. Evaporation due to convection is also more important on high porosity organic layers than on cooler bare mineral soil or burned humus (Johnson 1992; Smith 1951). Therefore, it usually has a lower water content than the other two seedbed types.

First-year mortality and seedbed thickness

Studies have shown that thick organic seedbeds, such as burned moss, which make up a large proportion of the seedbeds after a fire, often present important mechanical barriers to small germinants which need to penetrate them to get to an area of sufficient water content (Facelli and Picket 1991; Sydes and Grime 1918a,b; Waldron 1966). It might therefore be hypothesized that one of the most important factors influencing establishment and subsequent germinant survival is organic layer thickness. Studies have already shown that there are spatial patterns of organic layer consumption by fire in burn areas (St-Pierre *et al.* 1991; Weber *et al.* 1987; Dyrness and Norum 1983) and germination has also been found to be influenced by seedbed thickness (St-Pierre *et al.* 1991; Chrosciewicz 1976, 1974). However, little is known about how the proportions of the different seedbed types after a fire might affect recruitment. The relationship between germinant survival and organic layer thickness has never been clearly demonstrated. Studies that demonstrate an inverse relationship between organic layer thickness and germinant frequency (e.g. St-Pierre *et al.* 1991; Chrosciewicz 1974) do not take into account the proportion of the different types of seedbeds and, therefore, it is not clear whether the results are just an artifact of the frequency distribution of the seedbed types. There may be more germinants on mineral soil, for example, simply because mineral soil makes up a greater proportion of the total seedbeds. Clearly, we require the recruitment measurements to be in terms of germinant density rather than frequency or relative frequency, especially if we want to compare recruitment patterns between sites or between disturbance type.

In addition, seedbed receptivity decreases with time-since-fire (Fleming and Mossa 1995b; Paré *et al.* 1993: Foster 1985). Therefore, we might assume that age-specific mortality rates may be dependent on time-since-fire but little is known about the rates of organic layer accumulation on favourable seedbeds in the first few years after a fire.

There are two major problems with the field methodology used in studies of germinant establishment. The first one is related to the spatial scale at which the studies are often conducted. Seedbed thickness is often only measured at a few random points in a plot and the seedbed is assumed to be homogeneous over the entire plot (e.g. Duchesne and Sirois 1995; Chrosciewicz 1983). However, this is seldom the case; there are often favourable microsites within an unfavourable seedbed and the location of each germinant should therefore be carefully measured in order to accurately estimate the survival rate for a particular seedbed thickness. Effectively, the seedbed must be characterized at the spatial scale of the germinant. Hence, we need point measurements of seedbed characteristics instead of aerial measurements. The second problem is that studies are often conducted for a short period of time, leading to inaccurate estimates of survival rates. This is especially true in the boreal forest where survival rates can drastically change over the summer due to variation in precipitation. Estimating survival rates during a period of high precipitation, for example, will lead to an overestimation of survival rates on unfavourable seedbeds, because seeds may germinate but germinants are unlikely to survive when precipitation ceases for a few weeks (Zazada *et al.* 1983). Therefore, to accurately estimate the effects of seedbeds on germinant survival, seedbed distribution and proportions must be measured at a small spatial scale and survival must be measured at a large temporal scale.

First-year mortality and germinant size

It is clear that germinants need to penetrate organic layers to reach areas of high moisture which are found in the mineral soil and humus. It might therefore be hypothesized that another important factor influencing germinant survival is germinant length, or more specifically radicle length. The advantage of larger germinants has been demonstrated in many studies. Mortality due to drought decreases with an increase in seedling size (Cayford 1963; Day 1963). Longer taproots are also an advantage on dryer substrates (Day 1964). For example, if summer water availability becomes low before radicles reach a critical length, the germinants do not survive because they are incapable of reaching a zone of sufficient water (Foster 1985; Black and Bliss 1981). In the boreal forest, black spruce, which has a small germinant, has often been found to be more susceptible to dry conditions than jack pine, which has a larger germinant (Duchesne and Sirois 1995; Fleming and Mossa 1994; Sirois 1993; Day and Duffy 1963).

Germinant size

From the direct seeding literature, it is possible to predict survivorship in site prepared cuts using seed mass (Greene and Johnson 1997). Other studies have speculated on the relationship between survivorship and germinant length. If survivorship is affected by both seed mass and germinant length, we can hypothesize that there is a relationship between germinant length and seed mass. However, the relationship between seed mass and germinant length is still not clear, mainly because studies that have observed it did so indirectly, being principally interested in the effect of light on growth. Seed mass has been found to positively affect seedling height (Seiwa and Kikuzawa 1991; Foster and Janson 1985; Sorensen and Campbell 1985; Grime and Jeffrey 1965). However, the advantage is obscured when germinants are allowed to photosynthesize in deep shade; length then becomes a function of species-specific physiological responses to light (Leishman and Westoby 1984; Bazzaz 1979; Grime and Jeffrey 1965).

However, initial germinant length should be proportional to seed mass before significant photosynthesis of the cotyledons. There are two main components of seeds, the embryo and the endosperm, that determine the growth response during germination (Raven *et al.* 1992; Wright 1971 in Kozlwoski 1972). The endosperm provides nutrients to the growing embryo until it can photosynthesize, and the quantity of the food reserve available is related to the size of the seed, and hence to seed mass. Heavier seeds actually have more mitochondrial proteins which allows them to have higher respiration rates, and hence have a greater growth potential (MacDaniel 1969). If we assume the presence of an isometric relationship between seed mass and volume, then we expect the density of stems that differ in size to stay constant. This assumption leads to the expectation of geometric similitude between seed mass and linear lengths. The following germinant size measures: germinant length, hypocotyl length, radicle length and diameter, should therefore be proportional to seed mass raised to the power of 0.33 (Niklas 1994, 1992).

Summary and objectives

In summary, there is a need to accurately predict recruitment density after a disturbance in terms of easily measurable variables. To do so, we need accurate estimates of first-year survival of germinants, which I propose are a function of initial seedbed frequencies, germinant length and time-since-fire. I also propose that the establishment patterns of the germinants will be directly influenced by the spatial distribution of the seedbed types. The objectives of this study are then as follows:

1. To test the hypothesis that germinant size measures are proportional to seed mass raised to the power of 0.33.
2. To determine the frequencies of the different post-fire seedbed types.
3. To determine whether seedbed proportion and spatial distribution influence local recruitment patterns.
4. To determine germination and survival values of germinants on post-fire seedbeds and compare them to values on seedbeds present a few years after a fire.
5. The last objective of this study is to determine whether survival values and seedbed proportions can be used to estimate recruitment densities after disturbances.

METHODS

Study area

The field experiments and observations were conducted in an area located around Prince Albert National Park, Saskatchewan (53° 35' N to 54° 20' N and from 106° 0' W to 106° 47' W). This area is part of the Boreal Mixedwood Forest (Rowe 1972), so called because of the dominance of both deciduous species, white birch, *Betula papyrifera* March., balsam poplar, *Populus balsamifera* L. and trembling aspen, *Populus tremuloides* Michx., and coniferous species, balsam fir, *Abies balsamea* (L.) Mill., larch, *Larix laricina* (DuRoi) K. Koch., white spruce, *Picea glauca* (Moench) Voss, black spruce, *Picea mariana* (Mill.) B.S.P., and jack pine, *Pinus banksiana* Lamb.

The region has a gently rolling topography, with hills made up of glacial till or glaciofluvial materials. The climate is characterized by cool, short summers and long, cold winters. July and August are the warmest months of the year, and while there can be frost during any given month, there is an absence of frost for an average of 80 days during the year. Average annual precipitation ranges from 400 to 500 mm, 70% of which falls as rain.

The return time for fire in this region is less than 100 years. The three fires used in this study were all spring fires that were extinguished by rain. They are: the Bittern Creek fire which occurred on June 5, 1996 (see table 1 for site description), the Monday fire which occurred on June 12, 1995 (see table 2 for site description) and the Muskeg fire which occurred on May 10, 1989. Insect outbreaks have not been a major source of disturbance in this region during this century.

Allometric observations

I used six boreal and montane forest tree species, white spruce, black spruce, jack pine, larch, limber pine, *Pinus flexilis* (E. James) Rydb. and eastern white cedar, *Thuja occidentalis* L., to study the relationships between germinant length, radicle length and seed mass. I increased my sample size to examine the relationships between hypocotyl length, diameter width and seed mass by adding the measurements taken in a previous experiment (D. Greene, unpublished data) for white spruce (those measurements were combined with mine), balsam poplar, white birch, lodgepole pine, *Pinus contorta* Douglas ex Loudon and white pine, *Pinus strobus* L..

All the seeds were collected in the summer of 1996. Balsam poplar, white birch, white spruce, black spruce, larch and jack pine seeds were collected in the mixedwood boreal forest of central Saskatchewan. Limber pine and lodgepole pine seeds were collected in Kananaskis country, near Calgary, Alberta. Finally, white pine and eastern white cedar seeds were collected in the greater Montreal region, Quebec. Once collected, the seeds were kept in plastic bags at 5°C.

In my experiment, I first weighed 50 potentially viable seeds of the first six species using an electronic balance which was accurate to the nearest 0.001 mg. I then germinated the seeds on damp blotting paper in petri dishes placed in a 12 hour light regime at 22° C, an environment comparable to open field conditions. I watered and monitored the germination of the seeds daily. I removed the germinants from the petri dishes once the cotyledons emerged, in order to avoid important species-specific physiological responses to light. I then measured the hypocotyl lengths, radicle lengths (from which I obtained total lengths) and diameter widths (halfway along the hypocotyls) of all the germinants. All lengths were measured to the nearest millimeter using a ruler.

The other four species were germinated using similar methods but pots were used instead of petri dishes. The soil of the pots was kept moist for the duration of the observations, which usually did not last for more than a week, from the time of germination until the measurements were made. Therefore, I do not believe that this difference in technique affected the results. However, because the radicle lengths were not measured in that experiment, the results could only be used to the test the relationships between hypocotyl length, diameter width and seed mass.

Analysis

I log-transformed the data and used Model II power log regression analysis to determine the significance and the power log coefficients for the following relationships: 1) total germinant length versus seed mass, 2) hypocotyl length versus seed mass, 3) radicle length versus seed mass, and 4) diameter width versus seed mass. I used t-tests to test for differences between the slopes of the regression lines for germinant size measures versus seed mass, and that expected by allometry (0.33).

Finally, I used Model II regression analysis to analyze the data presented in table 1 of Seiwa and Kikuzawa (1991) and the data presented in tables 5 and 6 of Grime and Jeffrey (1965) to obtain the regression functions for the relationships between hypocotyl length and seed mass. I then used an ANOVA analysis to compare the slopes of those regressions to the one obtained with my data.

Relative densities in the field

I observed the natural occurrence of jack pine, black spruce, white spruce and trembling aspen germinants in the field using a transect study. In the Bittern Creek fire sites, I studied six transects: two jack pine transects in early August 1997, two black spruce transects in early August 1997, and two white spruce transects in mid-August 1997. In the Monday fire sites, I studied six transects: two jack pine, two black spruce and two trembling aspen transects in July 1997. In trembling aspen transects, I only counted sexual stems. I varied the size of my transects, from 1 m to 2 m in width and from 15 m to 30 m in length, depending on germinant density. For each transect, I mapped the position and diameter at the base of all standing and fallen trees. I also mapped the position of organic layer patches, and the location of all germinants. I noted the seedbed type on which each germinant was growing and measured its distance to the nearest tree bole. I also measured the depth to mineral soil, depth of the humus and O_f layers within one centimeter of the germinants by cutting a soil core using a soil corer or a sharp knife. In order to estimate the proportions of the different seedbeds in a stand, I measured depth to mineral soil, humus and O_f depths at every metre along the centre of the transects. I also measured the distance to the nearest tree bole every 50 cm along the center of the transects in order to get a regular distribution of distances to boles. The results of the two transects per site were combined for the analysis.

Analysis

1. Seedbed proportion

I estimated the proportion of mineral soil, humus by depth classes and organic layer by depth classes at each site by adding up the number of measurements of each seedbed type and dividing that number by the total number of independent points in a site (one per metre of transect).

2. Frequencies and relative densities

I first calculated the frequencies of germinants, the number of germinants on a particular seedbed, on mineral soil, humus by depth class and O_f by depth class. I then measured absolute density as the number of germinants per depth class divided by the transect area for that depth class. I defined relative density as the ratio of germinant density for a depth class over the germinant density on mineral soil. Finally, the relative densities of germinants (for all species) on O_f seedbeds were combined and a exponential regression analysis was used to determine whether there was a relationship between relative density and increasing O_f depth. The regression line was forced to pass through the origin because of the 1.0 relative density value on mineral soil.

3. Spatial distribution of the germinants

At each site, I first added the number of germinants in ten or twenty centimeter-wide annuli away from the nearest tree bole. I then calculated germinant density in each annulus by dividing the number of germinants by the transect area for that distance. I also calculated the number of germinants per metre square at each site and compared their distribution to a Poisson distribution using a chi-square test. I then used t-tests to determine whether the germinant distributions were clumped or superdispersed by testing whether the variance to mean ratios (dispersion coefficients) of the germinant spatial distribution were significantly different from one.

Germination and Survival

I performed viability tests on jack pine, black spruce and white spruce by germinating 100 seeds of each species on damp paper placed in petri dishes. I then corrected for percent germination in the following two experiments.

1. Pot experiments

I conducted a sowing experiment in pots where water was ample and, thus its lack was not a potential cause of mortality in germinants. I collected different seedbeds in the field and placed them in plastic pots of about 10 cm in diameter and 15 cm in depth. I ensured that the seedbed thicknesses were the same in each pot. I used 15 jack pine, black spruce and white spruce seeds in each of the following treatments: on top of mineral soil, on top of burned humus, on top of burned moss, on humus with burned needles, and on humus under an aspen leaf. There were three replicates of each treatment. I watered the pots four times a week to ensure that the seedbeds were kept moist at all time. I monitored germination and survival every week for about three months.

Analysis

I first tested the data for normality using Kolmogorov-Smirnov tests. I then used factorial model I ANOVAs for fixed factors to determine whether total germination and end-of-summer survival values were significantly influenced by seedbed type and/or species type, and to determine whether there were significant interactions between the two factors. I used Tukey post-hoc tests to test for significant differences between each treatment.

2. Sowing experiments in the field

In a field experiment I started in early June of 1997 (after snow-melt), I tested for differences in germination and survival values on different seedbeds, some present in recent burns and some present a few years after a fire. I used the following treatments: 1) at Bittern Creek, I placed 20 jack pine, 20 white spruce and 15 black spruce seeds on mineral soil, burned humus and burned moss in jack pine and black spruce stands, and on burned humus in a white spruce stand; 2) at Monday, I placed 15 jack pine, 15 white spruce and 10 black spruce seeds on burned humus, green-tongue liverwort (*Marchantia polymorpha*) and living moss (*Polytrichum juniperinum*) in jack pine and black spruce stands; 3) at Muskeg, I placed 15 jack pine, 15 white spruce and 10 black spruce seeds on *P. juniperinum* and aspen leaf litter in a black spruce stand, and on aspen leaf litter in a jack pine stand. The seeds were placed on top of the seedbeds. I replicated each treatment three times, ensuring that the thickness did not vary between the plots, which were about 20 by 20 centimeters in size. I monitored germination and survival weekly for three months.

Analysis

I first tested the normality of the data using Kolmogorov-Smirnov tests. Then, for each site, I used factorial model I ANOVAs for fixed factors to determine whether total germination and end-of-summer survival values were significantly influenced by seedbed type and/or species type, and to determine whether there were significant interactions between the two factors. Finally, I used Tukey post-hoc tests to test for significant differences between each treatment.

3. Permanent plots

Permanent plots were established at the end of the summer of 1996 to observe natural germination rates and subsequent survival of individual germinants in fire stands. Four 2m by 2m plots were set up in each of the following stands: jack pine and black spruce stands at Bittern Creek and Monday fire sites, where black spruce and jack pine germinants were observed, and a white spruce stand at Bittern Creek, where white spruce, black spruce and jack pine were observed. In each stand, two plots contained mostly mineral soil and humus seedbeds (over 90%) while the other two plots consisted mostly of organic layer seedbeds (over 90%). When the plots were established in 1996, the total number of germinants present in a plot were recorded. Starting in May 1996, I numbered and mapped each germinant and monitored individual survival every month, for four months. I combined the germinants of the four plots at each site for the analysis in order to increase the sample size.

Analysis

I first classified the germinants into two cohorts. First, a 1996, first-year cohort and a 1997, second-year cohort for the Bittern Creek fire. Next, a 1995-1996 cohort, since the first and second year cohorts were not initially separated and a 1997, third-year cohort for the Monday fire. The germinants that were present in May 1997 were placed in the first-year cohorts and any subsequent germination was placed in the second and third year cohorts. I then divided the germinants into two seedbed categories: those that were on mineral soil-humus and those that were on O_f seedbeds.

For the 1997 cohorts at each site, I obtained the total numbers of germinants per seedbed type and the numbers of new germinants on the two seedbed types, once a month for three months. The higher sample size for the sites in Bittern Creek allowed me to calculate survival curves for these sites. The curves represent the fraction of germinants that are alive as a function of age. For the Monday fire site, the survival of the 1997 and 1995-96 cohorts were observed as numbers per seedbed type for a period of four months because the sample sizes were too low to permit meaningful statistical analysis.

I then combined the data obtained for the jack pine and black spruce sites (at Bittern Creek) for jack pine and black spruce germinants to test for a differences in survivat on mineral soil plus humus and O_f seedbeds between the two species. I used a two-way model I ANOVA to test for seedbed, species and interaction effects.

Statistical methods

I conducted the Model II regression analysis as shown in Sokal and Rohlf (1995) and in Niklas (1994). I used the chi-square Goodness-of-fit to the Poisson distribution and the t-test for clumped distributions as shown in Zar (1996). I used the statistical package SPSS for all the other statistical analysis.

RESULTS

Allometric observations

For boreal and montane forest species (see Table 3 for mean values), a linear regression analysis (Table 4) demonstrated significant positive relationships between seed mass and germinant size measures. Seed mass accounted for 97% of the variance in germinant length ($p<0.001$), 94.2% of the variance in radicle length ($p<0.001$), 72.7% of the variance in hypocotyl length ($p= 0.002$) and 48.3% of the variance in diameter width ($p=0.026$). In addition, the power log regressions yielded slope values between seed mass and germinant length ($b=0.348$) and hypocotyl length ($b=0.340$) that were not statistically different ($p>0.2$) from the slope expected by allometry (0.33). However, the slope of the regression line between radicle length and seed mass ($b=0.467$) was significantly different from 0.33 ($p<0.02$), and the regression of diameter versus seed mass also yielded a slope value ($b=0.226$) that was slightly significantly different from the expected allometry ($p<0.05$).

In addition, regression analysis of hypocotyl length versus seed mass yielded a slope value ($b=0.340$) that was not significantly different ($p>0.2$) from that obtained using the data presented in Seiwa and Kikuzawa (1991) ($b=0.288$) and in Grime and Jeffrey (1965) ($b=0.389$).

Relative densities in the field

1. Relative frequencies of seedbeds

Not surprisingly, the relative frequency distributions of seedbed types presented in Figures 1 and 2 clearly demonstrated that there was important variability in seedbed proportions not only between fire years but between sites within a fire as well. However, a few general comments can be made. First, all the sites at Bittern Creek contained a higher proportion of O_f seedbeds than the sites at the Monday fire. In fact, there was no O_f in the black spruce site at Monday. Second, within the Bittern Creek fire sites (Fig. 1), the black spruce and white spruce sites had thicker organic layer seedbeds than the jack pine site. Next, mineral soil and humus made up, on average, about 50% of post-fire seedbed types at all sites. Finally, it can be noted that there was still a large proportion of mineral and humus seedbeds in the jack pine, black spruce and aspen sites, three years after the Monday fire (Fig. 2).

2. Frequencies and relative densities on humus

The frequencies of germinants decreased with increasing humus depth for all species (Figs. 3 and 4), expect for jack pine at the Monday fire site (Fig. 4b, c). However, the relationship between the density of germinants and increasing humus thickness (Figs. 5 and 6) was not clear. Mineral soil had the highest germinant density for only half the sites. The relative density on humus (all depths combined) ranged from 0.3 to 1.36 across all sites.

3. Frequencies and relative densities on organic layer

Mineral soil always had a higher frequency of germinants than O_f seedbeds (Figs. 3 and 4). Relative germinant density also tended to decrease as organic layer increases (Figs. 5 and 6). It is important to note that although all sites contained O_f seedbeds (Figs. 1 and 2), except for the black spruce site at Monday (Fig.2a), the numbers of germinants were always very low on those seedbeds. There were no aspen germinants present on organic layer seedbeds at the Monday fire site. When the relative densities of germinants at all sites were combined, I observed a significant relationship ($p<0.05$) in an exponential regression forced to pass through the origin ($b= -0.462$) (Fig. 7). Sixty-four percent of the variance in relative density was explained by O_f thickness. The relative density on O_f (all depths combined) ranged from 0.03 to 0.14 across all sites. I have little data on relative density on woody substrates (wood comprised only about 2% of the seedbeds, Figs.1 and 2), nonetheless they appeard to engender mortality rates as high as O_f seedbeds. Relative densities on wood ranged from 0 to 0.09 across all sites (Figs. 5 and 6).

4. Spatial distribution of germinants

Germinants tended to be distributed around tree boles (Figs. 8 and 9). There was a decrease in germinant density with increasing distance from the boles, although, germinants were sometimes not found right near the boles because of the presence of roots (pers. obs.). Fifty percent of the germinants of all species, except for white spruce, are found within 40 cm of the tree boles and 90% are found within 80 cm of the boles. In the white spruce site, 50% of the germinants are found within 53 cm of the boles and 90%

are found within 126 cm.

The goodness-of-fit to the Poisson distribution test (Table 5) demonstrated that the germinants were not randomly distributed at any site (all $p<<0.001$). In addition, the dispersion coefficient of the 8 sites (varying from 1.918 to 25.410) were all significantly greater than one (t-tests, $p<<0.001$), indicating that the spatial distributions of germinants were clumped.

Germination and Survival

1. Pot experiments

A. Germination

A two-way ANOVA demonstrated that the germination value was significantly influenced by seedbed type ($p=0.001$) but did not significantly differ among species ($p=0.321$). There was also no interaction between the two factors. The post-hoc Tukey test (Table 6) revealed that the mean germination value of seeds on humus (86%) was significantly higher than on burned moss (53%, $p=0.006$) and only slightly higher than on mineral soil (61%, $p=0.047$). Germination on mineral soil also was also significantly higher than on burned moss ($p=0.016$) but significantly lower than under a leaf (89%, $p=0.027$). Germination on burned moss was lower than on the leaf treatment ($p=0.003$). Finally, germination on the humus/needles treatment (83%) was slightly higher than on the burned moss treatment ($p=0.016$).

B. Subsequent survival

The factorial ANOVA revealed that germinant survival was significantly influenced by both seedbed type ($p<0.001$) and species ($p=0.018$). However, there was also a significant interaction between the two factors and therefore I could not perform post-hoc tests. The mean values for each treatment shown in Table 7 demonstrate that all species had a survival of 1.0 on the humus/needles treatment. Survival of jack pine germinants was highest on mineral soil (88%), followed by humus and moss (60%), and finally survival on the humus/leaves treatment was very low (12%). The survival of black spruce germinants was equal to 1.0 on mineral soil. Survival values on burned moss (83%) and leaves (74%) were also high, while survival was the lowest on humus (49%). The survival values of white spruce germinants werd also high on burned moss and leaves (about 80%), but contrary to the other species, they were lower on mineral soil (50%) than on humus (88%).

2. Sowing experiments in the field

A. Bittern Creek fire sites

The germination values at the jack pine site were not significantly different between species ($p=0.098$) but were between seedbeds ($p<0.001$). Germination values (Table 8) on humus and mineral soil were about the same (around 50%), but significantly greater than germination values on burned moss ($p<0.001$) and on humus/needles ($p<0.001$). In fact, no seeds germinated on burned moss and germination on the humus/needles seedbed was also very low (9.7%). The survival values of the germinants were also significantly influenced by seedbed type (p<0.001) and differed significantly between species (p=0.033). Survival values (Table 9) on mineral (83%) and humus (75%) were similar (p=0.847) but significantly greater than on humus/needles (p<0.001). Black spruce germinants had a survival rate similar to jack pine germinants (p=0.084) (although values for black spruce tended to be lower), and white spruce (p=0.936) . White spruce and jack pine germinants, on the other hand, had significantly different survival values (p=0.041).

Germination in the white spruce site was about 63% for black spruce and white spruce and about 27% for jack pine (Table 8). Survival values were about 49% for jack pine germinants, 71% for black spruce germinants and 65% for white spruce germinants (Table 9).

The germination values (Table 8) in the black spruce site were significantly different between species (p=0.001), between seedbeds (p=0.004) and there was also a significant interaction effect (p=0.005). Jack pine had high germination on mineral soil (91%) while the other two species had low germination on that seedbed (about 18%). Burned moss was a poor seedbed for all species but especially bad for white spruce (only 7% germination compared to 16% and 13%). Germination on humus/needles was approximately 50% for jack pine and black spruce but only 37% for white spruce. Finally, germination values on humus were higher for white spruce (49%) than for jack pine (39%), and lowest for black spruce (29%). Survival values, on the other hand, were only significantly different between seedbeds (p<0.001). Table 9 demonstrates that survival of germinants on humus/needles (75%) was not different from that on humus (93%, p=0.764) or on mineral soil (60%, p=0.330). Although germinant survival tended to be higher on humus than on mineral soil, the difference was not significant (p=0.056). Germinants on all three seedbeds had significantly higher survival values than those on burned moss (6%, p<0.001).

B. Monday fire sites

In the jack pine site, germination and survival values were quite low and did not differ significantly between the seedbeds; humus- 25%, *Marchantia polymorpha*- 11%, *P. juniperinum*- 18%, or between the species. Germination values in the black spruce site were significantly different between seedbeds (p=0.009) and between species (p=0.021). Germination (Table 10) on humus (9%) was similar to that on *M. polymorpha* (15%, p=0.719) but significantly lower than on *P. juniperinum* (33%, p=0.009). Germination on *M. polymorpha* was also slightly lower than the rate *P. juniperinum* (p=0.047). The survival values in that site were not different between seedbeds or between species. The average survival values of germinants were 20% on *M. polymorpha*, 9% on humus and 11% on *P. juniperinum* (Table 11).

C. Muskeg fire sites

In the jack pine site, only 5% of the white spruce seeds germinated on the litter layer (Table 12) and only 17% of them survived (Table 13). None of the jack pine or black spruce seeds germinated. In the black spruce site, only 38% of the jack pine seeds germinated on leaf litter and 35% of them survived. The average germination values were 39% on P. juniperinum and 13% on leaf litter. Germinant survival (Tables 13) was equal to 1.0 on *P. juniperinum*, which was significantly higher than survival on leaf litter ($p=0.011$) where the survival was 12%.

3. Permanent plots

A. 1996 cohorts

The changes in total number of germinants on mineral soil/humus and on O_f seedbeds are shown in Fig. 10 for the Bittern Creek sites and Fig. 11 for the Monday fire sites. There was always a higher number of germinants on mineral soil/humus than on O_f seedbeds. Jack pine also had a higher frequency than black spruce (Fig. 10b and 11b).

B. 1997 cohorts

There were more germinants in the black spruce and jack pine sites at the Bittern Creek fire sites (one year after burning, Fig. 12) than at the Monday fire sites (2 years after burning, Fig. 13). Figures 12 and 13 again demonstrate that there were more germinants on mineral+humus than on organic seedbeds for the 1997 cohorts. There was also a clear increase in the number of germinants early in the summer (with the exception of the black spruce site in the Monday fire), which then leveled off. This sharp increase is due to a high number of seeds germinating during the month of June (Figs. 14 and 15). Recruitment after July is low on all seedbeds, especially at the Monday fire sites, but it is always higher on mineral soil/humus than on O_f seedbeds.

The calculations of survival values for sites in the Bittern Creek fire demonstrate that late spring germinants experienced little mortality before the month of July, after which there was a sharp decline in survival (Figs. 16 and 17). The results also demonstrate that end-of-summer survival values were two times higher on mineral soil/humus (Fig. 16) than on O_f seedbeds (Fig. 17) for white spruce, jack pine and black spruce. A two-way ANOVA demonstrates that both jack pine and black spruce (no species effect, $p>.2$) had significantly higher survival on mineral soil/humus than on O_f seedbeds ($p<<.0005$).

Stage-specific survival

In the following section, I will attempt to use the survival values obtained in this study to predict recruitment densities. I will do this for jack pine at the Monday fire site as an example. In what follows, I assume that there is no fourth cohort as there were negligible amounts of seeds (about 1%) remaining in the cones of pines at Monday as of August 1997 (unpublished data). Also, I implicitly assume that the stage survival values are constant for all early cohorts. I will subdivide the recruitment dynamics of jack pine as a sequence of stages.

Essentially, the final recruitment density (F_D) prior to the onset of thinning should be:

$$F_D = (\text{Seed input})\, S_o S_{g1} S_w S_{g2}$$

where S_o is the survival of each seed cohort to the stage of censussed germinants after a late spring rainy season; S_{g1} is the survival of censussed germinants to the end of their first summer; S_w is their overwintering survival; and S_{g2} is the survival to the end of their second summer.

Averaging across the stage survival values of Monday and Bittern sites, and for the sowing experiments and permanent plots, I obtained the estimates for jack pine shown in Table 14. (I calculated the overwintering survivorship of that species using the number of jack germinants present in late August of 1996 at the jack pine site in the Monday fire site.) As can be seen, there is a steady rise in the stage survival values through time. Further, the differences in survival between the optimal seedbeds (mineral soil or humus) and O_f becomes muted by the second summer for a cohort.

I note that if I follow an imaginary cohort through two years, the cumulative survivorship ($S_oS_{g1}S_wS_{g2}$) would be 0.13 for mineral soil and humus and 0.023 for O_f. From the direct seeding literature, Greene and Johnson (1997) estimated juvenile survivorship for pine to be 0.02 in site-prepared clearcuts, where optimal seedbed coverage is typically only about 17% of the cut.

Because I do no have seed inputs for that site, I can predict the final pre-thinning density for pine (at a jack pine Monday fire site) by using the germinant densities found in the permanent plots at that site. The density of the first two cohorts is 2.13/m^2 (mineral plus humus) and 1.0/m^2 for O_f. I assume that there will be negligible subsequent losses for these two cohorts. By contrast, for the 1997 cohort (density of 1.38/m^2 on mineral/humus and 0.5/m^2 on O_f), I must multiply these values by the product $S_w S_{g2}$. Given that O_f comprises 33% of the seedbeds at the Monday pine site, the final pre-thinning density (averaged across all seedbed types) would be 2.2 stems per m^2. For a stand with this pre-fire basal area density (3.9m^2/ha), the regression of Greene and Johnson (1997) would predict a recruitment density of 1.35 stems per m^2.

DISCUSSION

Allometric observations

It is clear that seed mass positively influences initial germinant size measures (Table 3) as expected because of the use of internal seed reserves (Wright 1971 in Kozlowski 1972). However, the expected allometry between seed mass and germinant size measures was not always confirmed. There was no significant difference between the slope of total germinant length and seed mass and the expected slope of 0.33. The slope of hypocotyl versus seed mass was also not significantly different from 0.33, but it was a bit higher (0.340), while the slope of the regression of radicle versus seed mass was much greater than expected (0.467), suggesting that as seed mass increases, germinants put disproportionally more resources into radicles. The slope of the regression line between diameter and seed mass is also lower than 0.33, suggesting that germinants put more resources to increase in length than in girth.

Finally, the slope of the regression between hypocotyl length and seed mass was not significantly different from that obtained using the data presented in Seiwa and Kikuzawa (1991) and in Grime and Jeffrey (1965) for their experiments where light levels were the same as mine. The two studies were conducted for a longer period than mine, suggesting that even if true leaves and cotyledons are left to photosynthesize for a relatively short period of time, the allometric relationship will still hold. There are two possible reasons for this. First, the food reserves of the seeds may not be depleted very quickly, or second, photosynthesis rates of small germinants may be minimal. However, this remains to be tested.

These results indicate that seed mass in conditions of ample light does influence initial germinant size (prior to the deployment of the first true leaves), and more importantly it indicates that germinants put more resources into radicle length. The major implication on recruitment densities is that big-seeded species should be at a clear advantage in thick, high porosity, organic seedbeds. The allometric relationship between seed mass and germinant length will also have other important ecological applications. For example, it may be another explanation (other than life-history traits) why pioneer species, which are smaller in size than late-colonizers (Huston and Smith 1987; Finegan 1984; Bazzaz 1979), must germinate right away after a disturbance. In addition, different species must often compete for light with other individuals when they invade a site, and because big-seeded species will produce longer germinants, they should be at a great clear advantage.

Seedbed proportion and relative densities

I initially used the frequency distribution of germinants on different humus and O_f depths to directly compare with other studies. With the exception of the jack pine site at the Monday fire, germinant frequencies decreased with an increase in humus depth. This is similar to the results obtained by Chrosciewicz (1974), although his relationship was stronger than mine. I have reasons to believe, however, that he included O_f seedbeds in his regression and used "humus" as a term for all organic layers: his humus layers tended to be much thicker than those I observed at Bittern or Monday. Although most of my germinants tended to be on thin O_f and even in the case of trembling aspen, none of the germinants were found on O_f, I did not observe a decrease in germinant frequency with an increase in O_f depth, contrary to the results obtained by St-Pierre *et al.* (1991), Thomas and Wein (1985a) and Weber *et al.* (1987). There are two possible reasons why this might be the case. First, my sample size is small and my variation in depth classes is restricted. O_f layer consumption creates patches of exposed mineral soil and humus and O_f seedbeds. Thin O_f is very rare because it is only found in the transition zones between exposed humus or mineral soil and thick O_f. The other problem, which is probably the most important, is that these frequency values were only taken once during the summer and may not reflect true survivorship values. For example, the black spruce and jack pine sites at Bittern Creek were sampled in July after the (typically) heavy precipitation of June (pers. obs.). The O_f seedbeds contained enough moisture for seeds to germinate but these germinants have very high mortality until the end of the summer if they are on thick O_f, as shown in the sowing experiments and in the permanent plots. I also believe that for this reason, the frequency values of other studies are inflated.

Most studies only present the proportions of the different seedbeds as part of the site descriptions and the information is never used to calculate densities (e.g Zazada et al. 1983; Chrosciewicz 1974). When I switched from frequency to density, the recruitment picture changed. First, the relationship with increasing humus depth is no longer visible, while there is now a clear decrease in germinant density with increasing O_f depth. There is no obvious difference between density on mineral soil and density on humus, which suggests that the frequency differences observed previously were a result of differences in seedbed proportions. On the other hand, there is still a great difference in density between mineral soil and O_f seedbeds, suggesting actual survivorship differences.

There also does not seem to be a critical O_f depth, corresponding to the length of germinants, where germinants are no longer found. The potential advantage of longer germinants is therefore not clear in this case. Indeed, the boreal forest with its relatively small-seeded species is perhaps the worst place to evaluate this critical depth hypothesis. I had data for only jack pine, white spruce and black spruce, species with similar seed sizes. However, trembling aspen which has a very small seed was which interestingly not found on O_f seedbeds. Nonetheless, for the moment, I can merely state that humus and mineral soil are roughly equivalent seedbeds, while the cumulative survivorship of germinants on O_f seedbeds is on average about two times less just after the June rains, and about 6 times less by the end of the second summer.

My results clearly indicate that the proportions of O_f seedbeds vary by a factor of about three fold between sites (Fig. 1). This variation is a result of the differing degree of duff consumption by the fires. This process is dependent on many factors, such as moisture content and organic layer thickness, factors that vary greatly between sites (Johsnon 1992;

Dyrness and Norum 1983). The thinner O_f seedbeds observed in the jack pine sites are typical because these sites are usually dryer, while O_f tends to be thicker in black spruce sites (Johnson 1992).

This is also, to my knowledge, the first study that takes point measurements of seedbed depths and attempts to quantify the proportions of the different seedbeds after a fire. This will be very useful for making direct comparisons with the proportions present in site-prepared cuts where different scarification techniques are used.

Spatial distribution

The removal of the O_f layer around the tree boles is often observed after a fire (e.g. St-Pierre *et al.* 1991). It has been shown that duff consumption is more intense around tree boles (K. Miyanishi, unpublished data). This pattern of O_f consumption greatly influences the spatial establishment patterns of germinants, which are almost invariably always found clumped around the boles, indicating that because of the fires, the germinants establish in the same microsites as the parent trees. This association was also observed by St-Pierre *et al.* (1991). I basically see self-replacement of vegetation types at the scale of a few metres. Tree seedlings colonize the patches around burned boles. Shrubs and perennial herbs (via asexual reproduction) and bryophytes colonize the inter-bole spaces, which they had previously dominated (pers. obs.)

I corrected the germination rates for viability in the sowing experiments to ensure that the difference in germination values between the different species was not due to a difference in viability. Although the correction inflated the values, it also allowed me to make direct comparisons with other studies that had either ensured that all their seeds were viable (e.g. Zazada *et al.* 1983) or had also corrected for viability (e.g. Duchesne and Sirois 1995).

1. Pot experiment

In this experiment, humus (alone or with needles or leaves) was the best germination substrate, while mineral soil and burned moss were poorer seedbeds, although the differences were not great. One explanation for the similarity in values is that even if I watered the pots often, O_f seedbeds still dried up quickly and if the seeds did not sift their way down under the moss, they probably did not germinate. Mineral soil, on the other hand, might have been too compacted when it was placed in pots which might have impeded germination. Subsequent survival of the germinants was also influenced by seedbed type and the three species had different responses to the seedbeds. Nonetheless, the main conclusion of this experiment is that both germination and survival on high porosity organic substrates was much higher in the pots than in the field. This suggests that water availability is the prime cause of the difference in survival observed on different seedbed types in the field.

2. Sowing experiment

A. Bittern Creek fire sites

In the jack pine site, mineral soil and humus were the best seedbeds for both germination and survival, while burned moss and humus/needles were very poor seedbeds. These results are similar to many other sowing experiments (Fleming and Mossa 1995a, c, 1994; Fleming et al. 1995; Chrosciewicz 1976, 1974; Zazada et al. 1983). The humus/needles seedbeds were favourable in the black spruce and white spruce sites. The major difference for the black spruce site was that mineral soil was not a good germination seedbed. This higher germination on humus versus mineral soil was also observed by Duchesne and Sirois (1995) who speculate that germinants need some humus (organic material) to survive. However, it is not clear how humus should positively affect germination. In my case, the difference may be due to the fact that the black spruce site was so wet that the mineral soil plots were submerged in water for part of the summer, which might have negatively affected germination.

B. Monday fire sites

Germination and survival on humus were lower in the black spruce and jack pine sites than the sites at Bittern Creek. This is probably due to the dryness of the sites (they are higher above the water table than at the Bittern Creek sites). I can, however, only speculate on the actual cause of this difference since I did not measure soil water content in this study.

Germination and survival on *M. polymorpha* were also low but better than on the humus seedbeds. This may be due to the fact that the liverwort may have retained more water than the blackened humus surface.

Germination and survival were best on *P. juniperinum*, where seeds may have been exposed to higher water contents (because the soil was not exposed to direct sunlight) and protected from granivores. This confirms the results of other studies that have found thin mosses to be good germination seedbeds (Groot 1996; Fleming and Mossa 1995b, 1994; Fleming *et al.* 1995; Groot and Adams 1994; Chrosciewicz 1976).

The results of the sowing at the Monday sites demonstrate that the seedbeds present three years after a burn, humus, mosses and liverworts, are still quite favourable for germination and survival of the germinants. The very low observed density of 1997 germinants at that fire must therefore be due to the depletion of the aerial seed banks.

C. Muskeg fire sites

Eight years following a fire, the forest floor is covered primarily by either *P. juniperinum* or aspen leaf litter, while mineral soil and humus seedbeds no longer exist. The moss is still a good seedbed but leaf litter, on the other hand, proves to be a very poor seedbed. Only a few jack pine and white spruce seeds germinated and survived on that seedbed. This is probably due to the fact that, while seeds may germinate readily under the leaves (as shown in the pot experiment), short hypocotyls cannot penetrate thick litter layers (Facelli and Picket 1991). On the other hand, if seeds remain on top of a leaf, they will probably never get enough moisture to germinate (as I observed in a preliminary pot experiment).

This experiment demonstrates that 8 years after a fire, the receptivity of the seedbeds has tremendously decreased. Fleming and Mossa (1995b) also demonstrate that 5 years after a cut, about 50-95% of the seedbeds (depending on the site) are no longer favourable for germination. We need to study more (natural) fires, or longer permanent plots, to understand the rate at which seedbeds deteriorate. However, it will be difficult to generalize since the processes of litter accumulation and decomposition will be dependent on factors such as water content, and hence will be site-specific.

3. Permanent plots

A. 1996 cohorts

The 1996 cohorts in Bittern Creek contained very few individuals compared to the 1997 cohort, indicating that either most seeds did not abscise the year of the fire or that most seeds delayed germination until the following summer.

The black spruce plots at the Monday fire only had two jack pine and one black spruce germinant in 16 m^2, three summers after the fire occurred, which is obviously very low. This again demonstrates the great variability between sites. The actual survival estimates (Fig.11) are not different from the other sites. This leads me to believe that the low density of this cohort is due to a lower total seed input at that site. The site was effectively a small "island" of black spruce trees surrounded by a bog on one side and pine and trembling aspen trees on the other side (per. obs.).

B. 1997 cohorts

The densities of all the germinants were much higher on mineral soil and humus than on O_f seedbeds. This confirms the results found in the sowing experiments and in the relative density observations from the transect study. These estimates translate into survival values that are much higher on mineral soil and humus than on O_f seedbeds for white spruce, jack pine and black spruce. In fact, there was no difference in survival values between jack pine and black spruce, which contradicts the results of Sirois (1993) and Chrosciewicz (1976) who report that jack pine usually does better than black spruce on all seedbeds.

In addition, the data collected in the plots demonstrates that most seeds germinate during the month of June (Figs. 14 and 15), after which point there is very little recruitment. This is often observed in the boreal forest (e.g. Zazada *et al.* 1983) and is probably due to the fact that summer rainfall typically peaks in June. However, this may vary between years and between sites depending on the weather patterns; on relatively warmer sites (or years) for example, germination could be greater earlier in the season. Survival of germinants is initially virtually 1.0 until after this rainy period, and then subsequently declines with each census during the summer as shown by Duchesne and Sirois (1995).

Stage-specific survival

My estimate of total pre-thinning recruitment densities after a disturbance was within less than two-fold of the prediction of Greene and Johnson (1997), and given the scatter of their power law regression this is very close agreement. The scatter of their regression line is essentially due to the fact that survival on different seedbeds is not taken into account: for example, their estimate will be close to the observed if the site contained mostly mineral soil but not close if the site contains mainly organic seedbeds. Therefore I believe that by adding a survival term in the equation (which already takes into account seed inputs) gives a closer estimate of recruitment density.

In addition, because I can estimate survival and recruitment as a function of seedbed type, I can now more easily compare with other types of disturbances. As I mentioned previously, Greene and Johnson (1997) predict germinant survival to be about 0.02 on site-prepared cuts where exposed mineral soil and humus represent only about 15% of available seedbeds. Therefore, in order to successfully regenerate a cut by natural regeneration, the amount of humus and mineral seedbeds will have to be increased.

GENERAL CONCLUSIONS

The broad conclusions of this study will be presented here with particular emphasis on jack pine and black spruce as they constitute the bulk of the data set.

1. Germinants of jack pine, black spruce and white spruce are preferentially located near burned boles because mineral soil and humus are aggregated around boles. This spatial pattern is likely due to differential duff consumption near boles and not seed inputs because at this scale, there will be no obvious seed shadow effect due to seed dispersal patterns (at least for jack pine and black spruce). While there are clear differences in O_f as a proportion of surface area among sites and fires, nonetheless, the proportion of substrates which are O_f does not vary by more than three-fold among my sites. Thus, much of the variance in survivorship of the sexual recruitment will occur at the scale of inter-bole distances (a few metres). In consequence, much of the variation in reported values of survivorship may be due to quadrat placement and number rather than to intrinsic differences in site characteristics, fire intensity, or recent precipitation regime.

2. Although an allometric relationship was observed between seed mass and germinant length, the potential advantage of larger germinants is still not clear in this system. However, there is evidence that O_f thickness does influence early establishment.

3. The aerial seed bank of jack pine is depleted by the middle of the third summer.

Consequently, only three main cohorts will arise (a fourth cohort should be quite small). Much of the seed bank abscises in the first summer, but a large fraction of these seeds defer germination to the second summer. The size of this fraction may well vary from one fire to the next, depending on the fire date and the seasonal rainfall. Black spruce, likewise, should essentially only have three cohorts because, as with jack pine, I have found virtually no seeds remaining in the cones by the third summer.

I note that for both these two species many studies have shown broad age class distributions (e.g. St-Pierre et al. 1992) or even a delay in recruitment when old fires are examined (e.g. Morneau and Payette, 1989; Sirois and Payette 1989). Therefore, the age determinations in these studies must be in error (see Desrochers and Gagnon 1997). The combination of seed bank exhaustion and the apparent inability of these species to defer post-abscission germination beyond one year leads to the conclusion that there will be, effectively, only three cohorts in the immediate aftermath of a fire.

4. For jack pine at the Monday fire site, I have advanced a simple stage-specific mortality argument. I view it as a sequence of four stages. In the first stage, recently abscised seeds or overwintering seeds begin to germinate in late May and the numbers of germinants increase as the rainfall peaks in late June. For this cohort, at this stage, the survival from abscission to germination is about two times higher on mineral soil and humus than on O_f seedbeds. Very broadly, survival declines with O_f depth. The next stage is from the end of the rainy period to the cessation of growth in early September. During this second

period, survival is about two times higher on mineral soil/humus than on O_f.

The net multiplicative effect of these first two stage-specific survival is that the end-of-summer survival is about four times higher on mineral soil and humus than on O_f. The cause of the differential survival is thought to be water availability. As the pot experiment showed, when water is not limiting germination or survival, there is much higher end-of-summer survival on O_f in pots than in the field.

The third stage is overwintering stem mortality. Here I have little evidence that seedbed type or O_f thickness plays any role. The cause of death (needle ice? post-snowmelt mortality prior to the next spring census?) is not known. However, about half the stems die during this period.

Finally, the stems entering their second summer appear to suffer much lower mortality than in the first summer. I speculate that the survival over the next few years (until they are tall enough to begin thinning) will be near 1.0.

RECOMMENDATIONS FOR SUBSEQUENT RESEARCH

I will assume that we are seeking predictive arguments for pre-thinning recruitment densities. I will assume further that we want to apply these equations to harvested tracts so that we can understand the optimization of cut diameter (as cuts become wider, the harvesting cost/ha declines, but the cost of artificial regeneration increases).

First, we need permanent plots that continue for at least five years to test my hypothesis that survivorship is near 1.0 beginning the third summer. I expect that whatever mortality occurs will be independent of O_f thickness. For the species lacking aerial seed banks, I expect that the accumulation of leaf litter (for sites close to aspen stands) will limit the recruitment episode to about five cohorts. Clearly, continued sowing experimentation near the permanent plots will greatly aid the testing of this hypothesis.

Second, we need to compare the frequency distribution of O_f thickness found in clearcuts and stripcuts to those found in fire sites. I know of only two studies on the exposure of mineral soil and humus in site-prepared cuts in the west, and these indicate that scarification results in four times less exposure than wildfires (Fleming et al. 1987) and prescribed burning is five times less (Chrosciewicz 1983). In short, the tendency for inadequate natural regeneration in harvested tracts may be due to inadequate site preparation (in addition to the obvious dispersal constraint).

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Table 1. Description of Bittern Creek fire study sites. These values are based on the transect study measurements.

	Black spruce	**Jack pine**	**White spruce**
Total density (stems/m^2)	0.933	0.577	0.353
Black spruce	0.925	0.394	0.309
Jack pine	0.008	0.183	-
White spruce	-	-	0.044
Total basal area/area (m^2/m^2)	7.485 X 10^{-4}	8.804 X 10^{-4}	1.196 X 10^{-4}
Black spruce	7.483 X 10^{-4}	4.613 X 10^{-4}	5.891 X 10^{-4}
Jack pine	2.487 X 10^{-7}	4.191 X 10^{-4}	-
White spruce	-	-	6.070 X 10^{-4}
Proportion of species (%)			
Black spruce	99.11	68.33	87.5
Jack pine	0.89	31.67	-
White spruce	-	-	12.5

Table 2. Description of Monday fire study sites. These values are based on the transect study measurements.

	Black spruce	**Jack pine**
Total density (stems/m^2)	1.35	1.22
Black spruce	1.25	1.07
Jack pine	0.08	0.13
Trembling aspen	0.02	0.02
Total basal area/area (m^2/m^2)	8.416×10^{-4}	9.601×10^{-4}
Black spruce	5.729×10^{-4}	5.887×10^{-4}
Jack pine	2.518×10^{-4}	3.885×10^{-4}
Trembling aspen	1.696×10^{-5}	1.353×10^{-5}
Proportion of species (%)		
Black spruce	92.6	87.7
Jack pine	6.2	11.0
Trembling aspen	1.2	1.3

Table 3. Measurements for allometric observations presented as species means ± standard errors. Lengths are in millimeters and seed masses are in milligrams.

Species	n	Seed mass	Total length	Hypocotyl length	Radicle length	Diameter width
B. papyrifera	8	0.213±0.035	-	14.225±0.938	-	0.525±0.045
L. laricina	13	1.916±0.061	31.692±2.052	19.538±1.483	12.154±1.818	0.700±0.036
P. balsamea	2	0.850±0.05	-	10.000±1.000	-	1.000±0
P. banksiana	21	3.879±0.129	50.429±1.888	26.523±0.999	23.904±1.540	0.890±0.030
P. contorta	12	4.550±0.722	-	32.583±7.695	-	0.783±0.037
P. flexilis	12	80.275±7.566	131.250±7.355	48.500±3.336	82.250±5.977	1.792±0.116
P. glauca	12	2.827±0.089	43.083±2.966	25.500±1.530	17.583±1.716	0.896±0.043
*P. glauca**	23	2.601±0.103	-	30.139±1.530	-	0.798±0.035
P. mariana	19	1.211±0.031	35.053±1.198	19.211±0.804	15.821±0.627	0.474±0.015
P. strobus	5	18.462±2.211	-	71.880±8.233	-	1.040±0.024
T. occidentalis	28	14.071±0.684	78.857±2.46	33.357±1.433	45.500±2.461	0.606±0.010

Note: * represents combined data from two experiments.

Table 4. Model II regression analysis for the allometric observations of boreal and montane forest tree species. L is germinant length, h is hypocotyl length, r is radicle length, d is diameter width and m is seed mass (all lengths are in millimeters and seed masses are in milligrams).

Regressions	N	r^2	Anova p value	95% confidence of slope	95% confidence of intercept	Functions
L vs m	6	0.970	<0.001	0.264 - 0.432	1.393 - 1.555	$L=29.814m^{0.348}$
r vs m	6	0.942	0.001	0.357 - 0.577	1.052 - 1.264	$r=14.038m^{0.467}$
h vs m	10	0.727	0.002	0.195 - 0.485	1.100 - 1.360	$h=16.999m^{0.340}$
d vs m	10	0.483	0.026	0.093 - 0.359	-0.337 - (-0.099)	$d=0.606m^{0.226}$

Table 5. Coefficients of dispersion and chi-square values for the Goodness-of-fit to the Poisson test and t-tests for germinant distributions. Bs is black spruce, Jp is jack pine, Ws is white spruce and Ta is trembling aspen. Bittern and Monday represent Bittern Creek and Monday fire sites, respectively.

Site	Coefficients of dispersion	chi-square	p value (chi-square)	p value (t-test)
Bs- Bittern	7.780	160.422	<< 0.001	<< 0.001
Jp-Bittern	5.878	202.114	<< 0.001	<< 0.001
Ws-Bittern	7.752	541.551	<< 0.001	<< 0.001
Bs-Monday	1.918	43.057	<< 0.001	<< 0.001
Jp-Monday	2.781	122.324	<< 0.001	<< 0.001
Ta-Monday	25.410	108.303	<< 0.001	<< 0.001

Table 6. Mean germination values for pot experiment (values represent the averages of three replicates).

Species/ Seedbed	Humus	Mineral soil	Burned moss	Humus + needles	Humus + leaf
Jack pine	0.921	0.542	0.685	0.875	0.875
Black spruce	0.714	0.778	0.381	0.730	0.825
White spruce	0.958	0.507	0.534	0.889	0.959
Average	0.864[a]	0.609[bc]	0.533[b]	0.831[ac]	0.886[a]

Note: a, b, and c represent significant differences detected by Tukey post-hoc test.

Table 7. Mean survival values for pot experiment (values represent the averages of three replicates).

Species/ Seedbed	**Humus**	**Mineral soil**	**Burned moss**	**Humus + needles**	**Humus + leaf**
Jack pine	0.621	0.880	0.590	1.0	0.115
Black spruce	0.486	1.0	0.806	1.0	0.838
White spruce	0.879	0.497	0.833	1.0	0.738
Average	0.662	0.792	0.743	1.0	0.564

Table 8. Mean germination values for field sowing experiment at Bittern Creek fire sites (values represent the averages of three replicates).

Site	Species	Humus	Mineral soil	Burned moss	Humus+ needles
Black spruce	jack pine	0.386	0.911	0.163	0.569
	black spruce	0.286	0.190	0.127	0.508
	white spruce	0.486	0.171	0.069	0.365
	Average	0.386	0.424	0.120	0.481
Jack pine	jack pine	0.468	0.508	0	0.203
	black spruce	0.508	0.158	0	0
	white spruce	0.365	0.451	0	0.087
	Average	0.447[a]	0.372[a]	0[b]	0.097[b]
White spruce	jack pine	-	-	-	0.271
	black spruce	-	-	-	0.650
	white spruce	-	-	-	0.620
	Average	-	-	-	0.514

Note: a and b represent significant differences detected by Tukey post-hoc tests.

Table 9. Mean end-of-summer survival values for field sowing experiment at Bittern Creek fire sites (values represent the averages of three replicates).

Site	Species	Humus	Mineral soil	Burned moss	Humus+ needles
Black spruce	jack pine	0.846	0.833	0.066	0.949
	black spruce	1.0	0.5	0.111	0.497
	white spruce	0.944	0.467	0	0.808
	Average	0.930[a]	0.600[a]	0.059[b]	0.751[a]
Jack pine	jack pine[a]	0.849	1.0	0	0.5
	black spruce[a]	0.586	1.0	0	0
	white spruce[b]	0.806	0.494	0	0.167
	Average	0.747[a]	0.831[a]	0[b]	0.222[b]
White spruce	jack pine	-	-	-	0.492
	black spruce	-	-	-	0.712
	white spruce	-	-	-	0.648
	Average	-	-	-	0.617

Note: a and b represent significant differences detected by Tukey post-hoc tests.

Table 10. Mean germination values for field sowing experiment at Monday fire sites (values represent the averages of three replicates).

Site	Species	Humus	*M. polymorpha*	*P. juniperinum*
Black spruce	jack pine[a]	0.244	0.109	0.488
	black spruce[b]	0	0.143	0.048
	white spruce[b]	0.023	0.185	0.463
	Average	0.089[a]	0.146[a]	0.333[b]
Jack pine	jack pine	0.484	0.081	0.244
	black spruce	0.095	0.191	0.095
	white spruce	0.162	0.069	0.208
	Average	0.247	0.114	0.182

Note: a and b represent significant differences detected by Tukey post-hoc tests.

Table 11. Mean in end-of-summer survival values for field sowing experiment at Monday fire sites (values represent the averages of three replicates).

Site	Species	Humus	*M. polymorpha*	*P. juniperinum*
Black spruce	jack pine	0.167	0.167	0.268
	black spruce	0	0.333	0
	white spruce	0	0.095	0.067
	Average	0.056	0.198	0.112
Jack pine	jack pine	0.426	0.667	0.333
	black spruce	0	0.667	0.333
	white spruce	0.333	0.5	0.300
	Average	0.380	0.611	0.322

Note: a and b represent significant differences detected by Tukey post-hoc tests.

Table 12. Mean germination values for field sowing experiment at Muskeg fire sites (values represent the averages of three replicates).

Site	Species	*P. juniperinum*	Aspen leaf litter
Black spruce	jack pine[a]	0.461	0.380
	black spruce[a]	0.476	0
	white spruce[b]	0.232	0
	Average	0.390[a]	0.127[b]
Jack pine	jack pine	-	0
	black pruce	-	0
	white spruce	-	0.046
	Average	-	0.015

Note: a and b represent significant differences detected by Tukey post-hoc tests.

Table 13. Mean end-of-summer survival values for field sowing experiment at Muskeg fire (values represent the averages of three replicates).

Site	Species	*P. juniperinum*	Aspen leaf litter
Black spruce	jack pine	1.0	0.348
	black spruce	1.0	0
	white spruce	1.0	0
	Average	1.0[a]	0.116[b]
Jack pine	jack pine	-	0
	black spruce	-	0
	white spruce	-	0.167
	Average	-	0.056

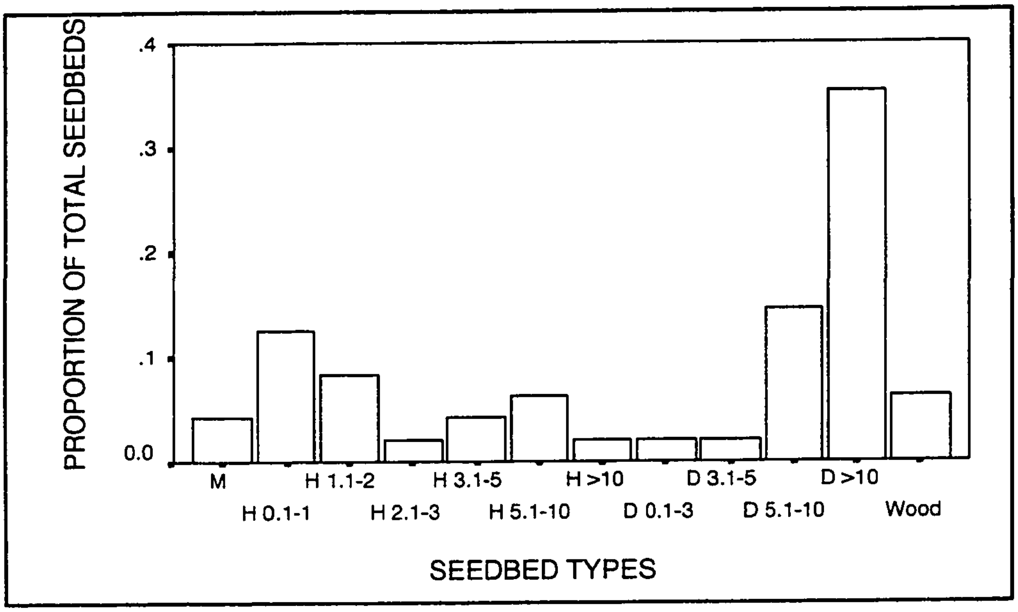
Note: a and b represent significant differences detected by Tukey post-hoc tests.

Table 14. Survival values of jack pine germinants at Monday fire site obtained from the different experiments conducted in this study. S_o is the survival of each seed cohort to the stage of censussed germinants after a late spring rainy season; S_{g1} is the survival of censussed germinants to the end of their first summer; S_w is their overwintering survival; and S_{g2} is the survival to the end of their second summer.

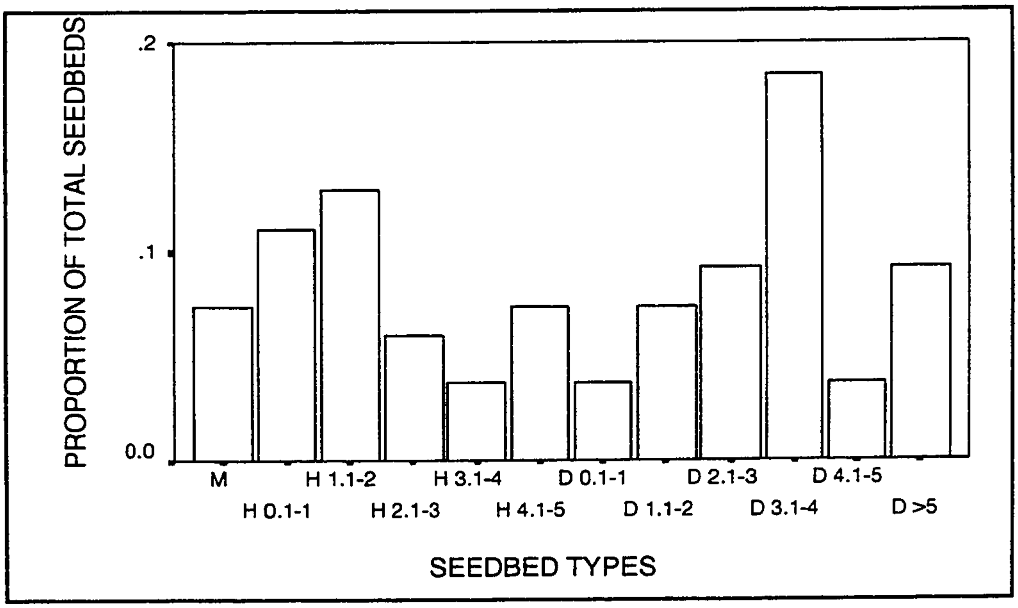
Survival / Seedbed	**Mineral soil and Humus**	**Organic layer**
S_o	0.39	0.16
S_{g1}	0.63	0.34
S_w	0.61	0.62
S_{g2}	0.87	0.69
Cumulative	0.13	0.023

Figure 1. Proportion of seedbed types at Bittern Creek fire sites. M represents mineral soil, H represents humus, D represents O_f and wood represents decayed wood. Humus and O_f seedbeds are divided into depth classes (cm).

a. Black spruce site



b. Jack pine site



c. White spruce site

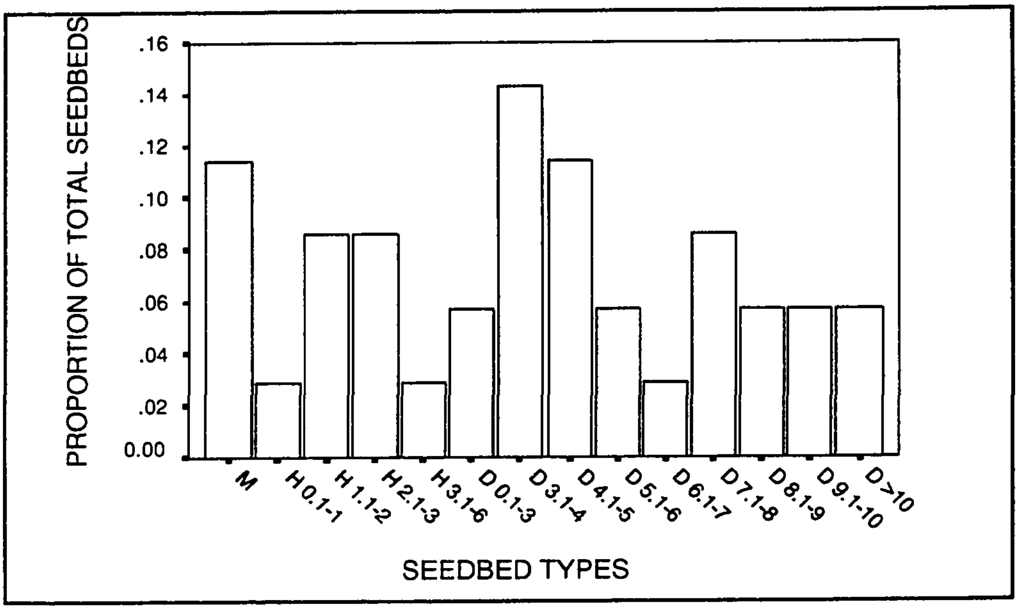
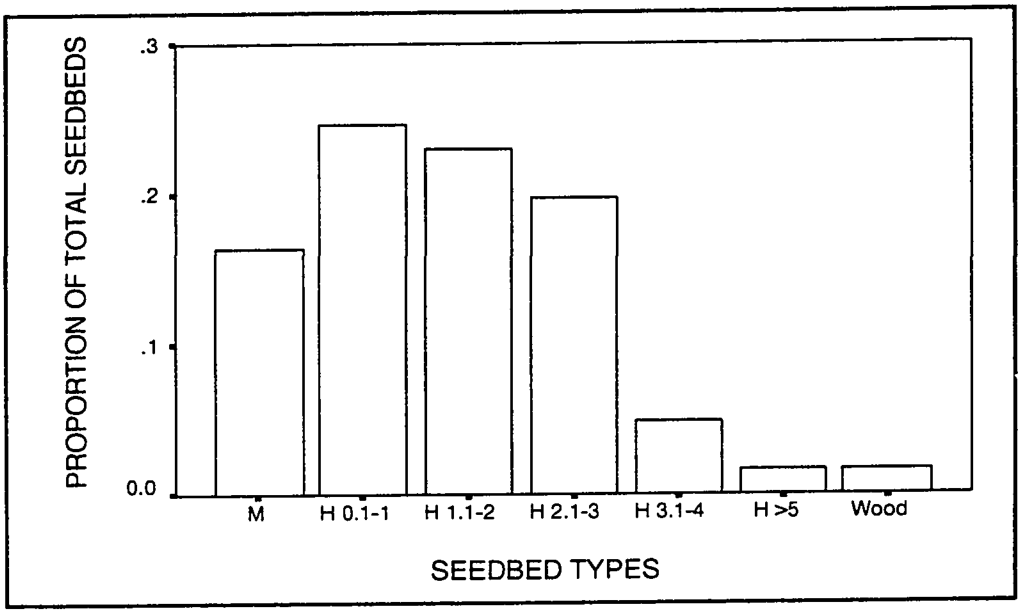
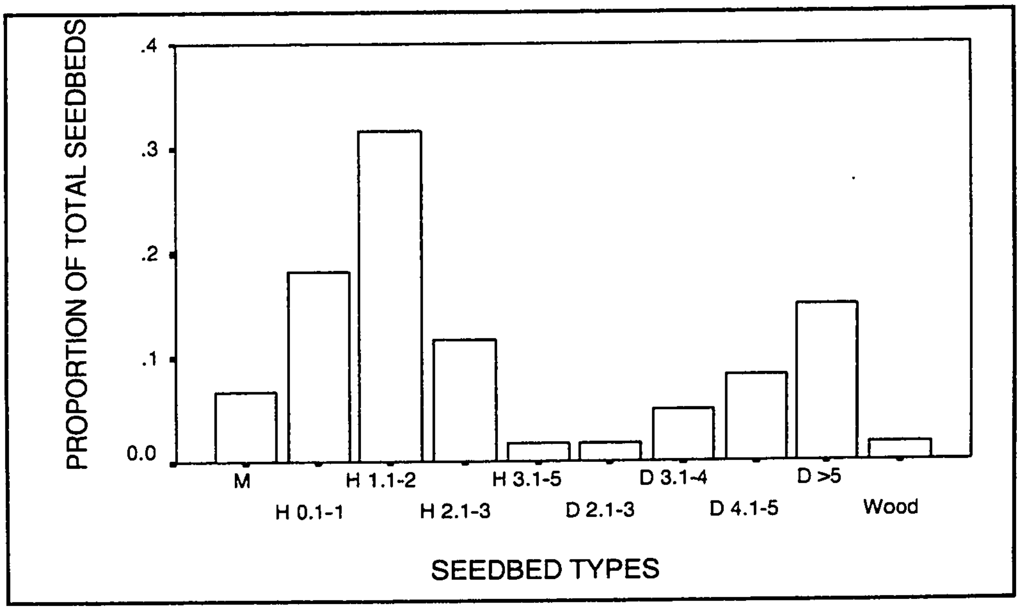


Figure 2. Proportion of seedbed types at Monday fire sites. M represents mineral soil, H represents humus, D represents O_f and wood represents decayed wood. Humus and O_f seedbeds are divided into depth classes (cm).

a. Black spruce site



b. Jack pine site



c. Trembling aspen site

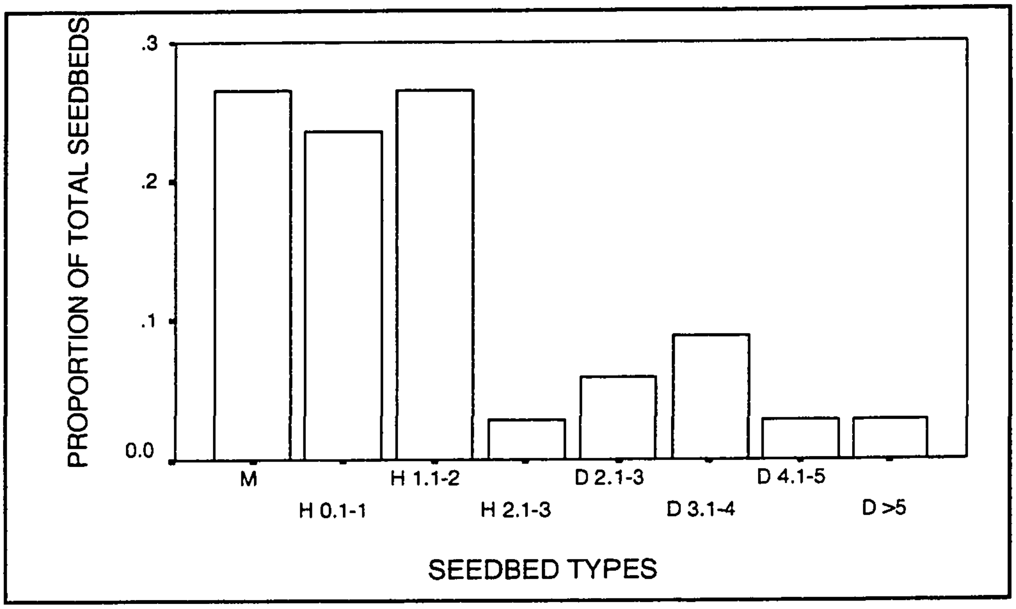
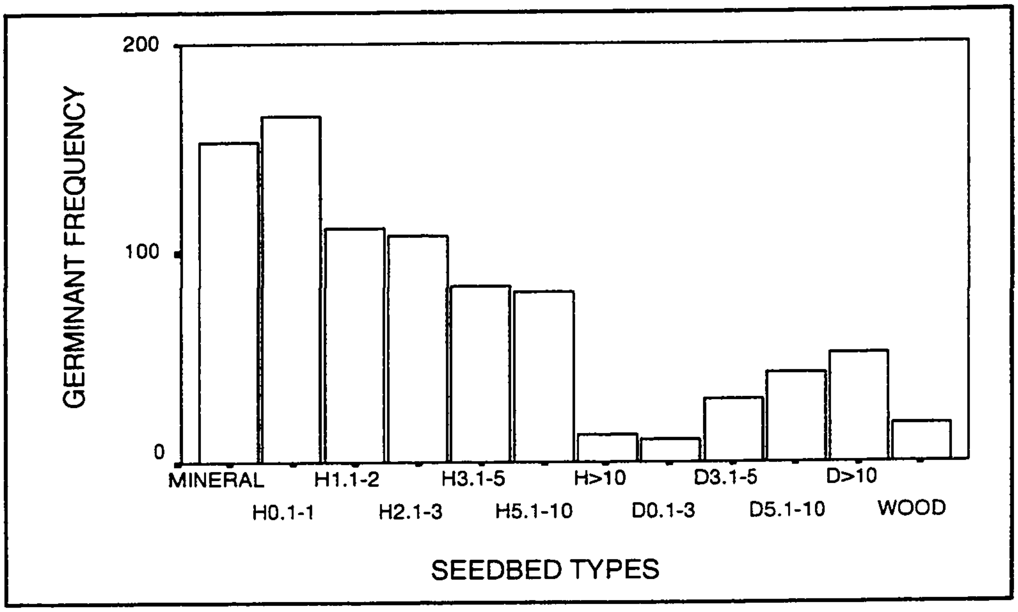
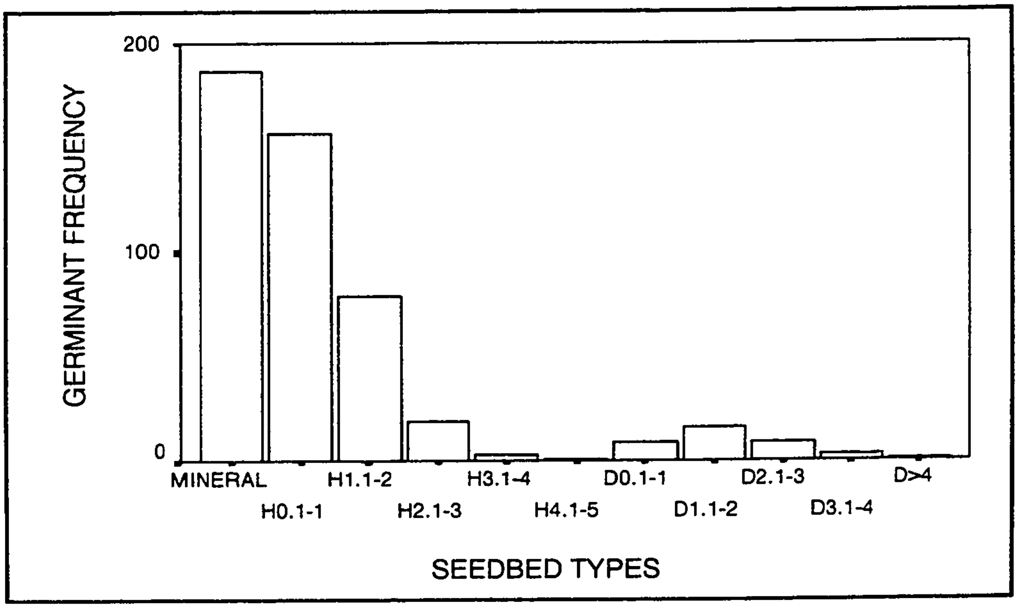


Figure 3. Frequency of germinants on mineral soil, humus (H), O_f (D) and decayed wood (wood) seedbeds at Bittern Creek fire sites. Humus and O_f seedbeds are divided into depth classes (cm).

a. Black spruce site



b. Jack pine site



c. White spruce site

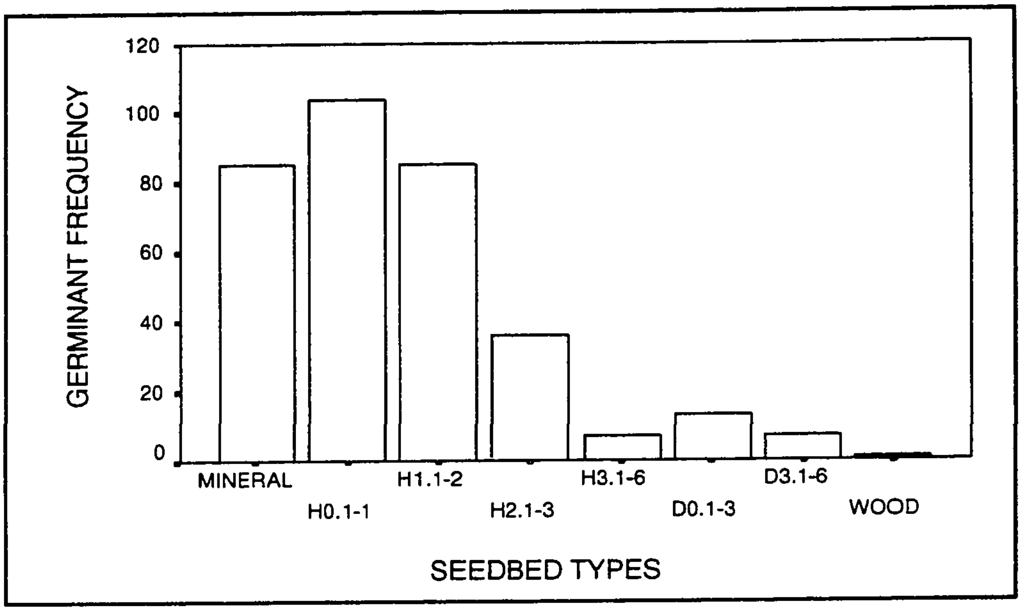
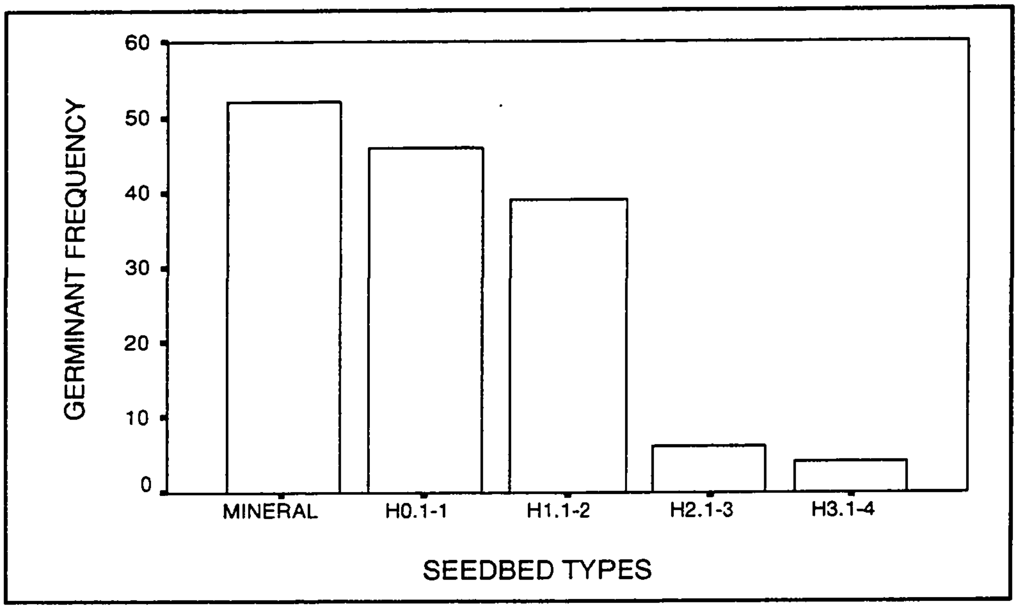
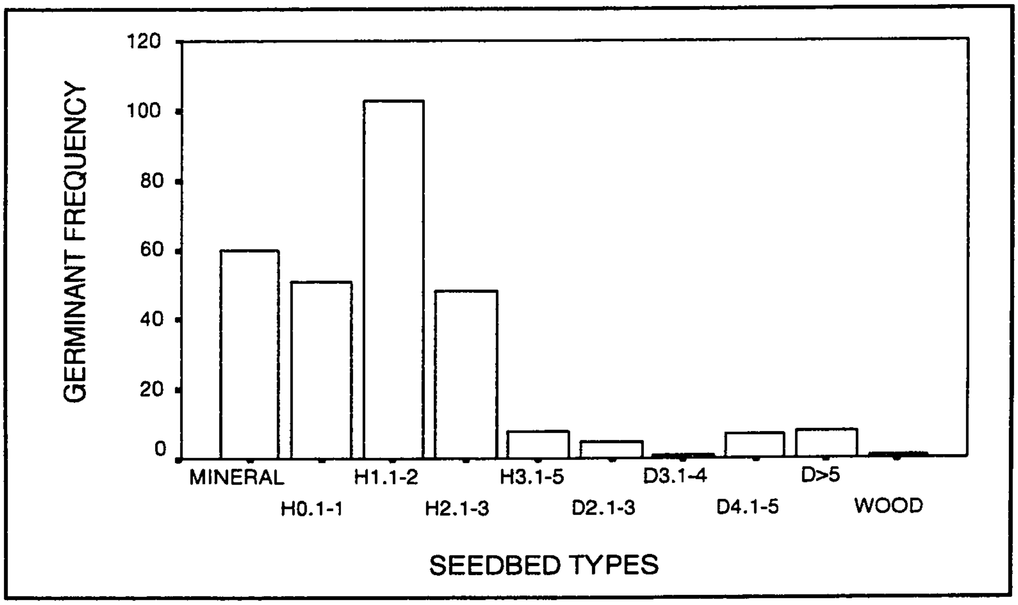


Figure 4. Frequency of germinants on mineral soil, humus (H), O_f (D) and decayed wood (wood) seedbeds at Monday fire sites. Humus and O_f seedbeds are divided into depth classes (cm).

a. Black spruce site



b. Jack pine site



c. Trembling aspen site

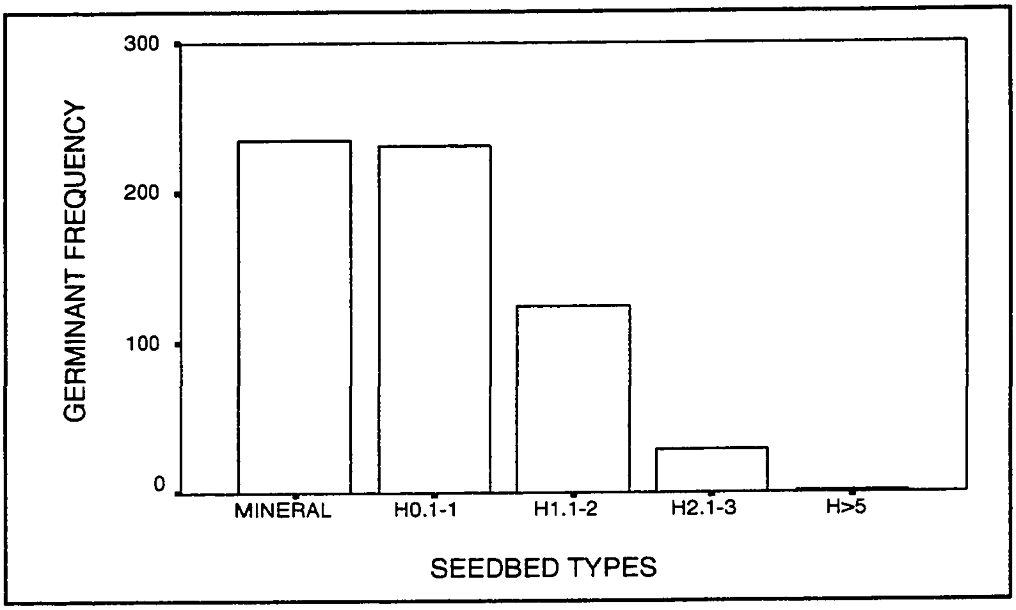
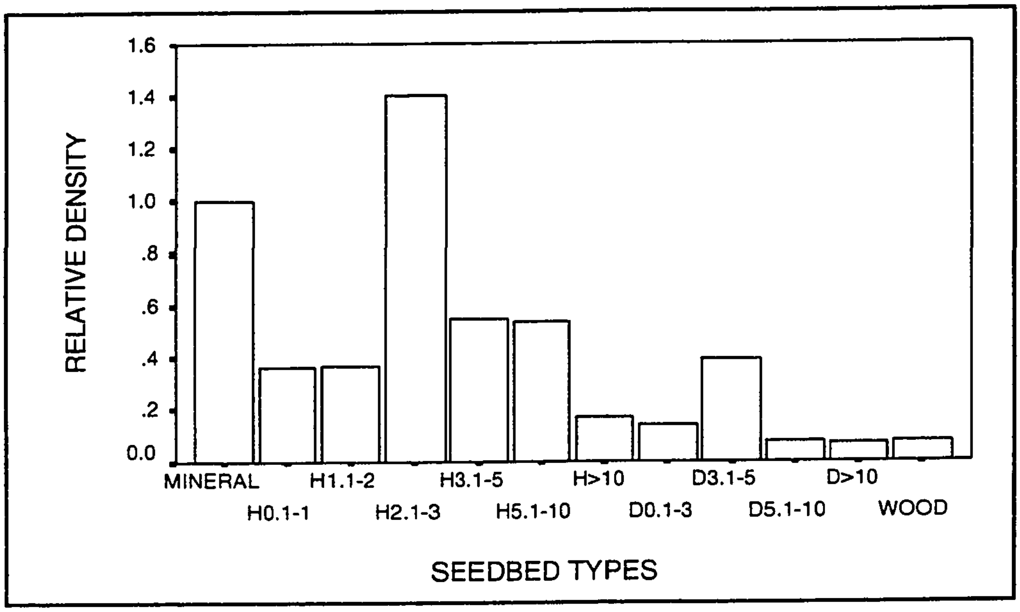
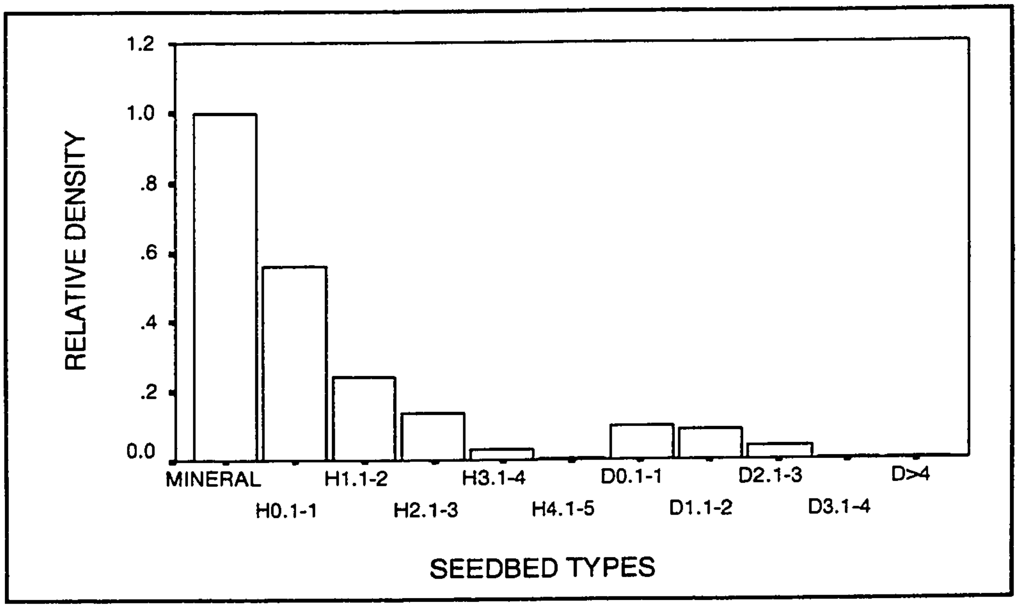


Figure 5. Relative densities of germinants on mineral soil, humus (H) and O_f (D) seedbeds (divided into depth classes), and decayed wood at Bittern Creek fire sites. Relative density is defined as the ratio of germinant density for a depth class over the germinant density on mineral soil.

a. Black spruce



b. Jack pine site



c. White spruce site

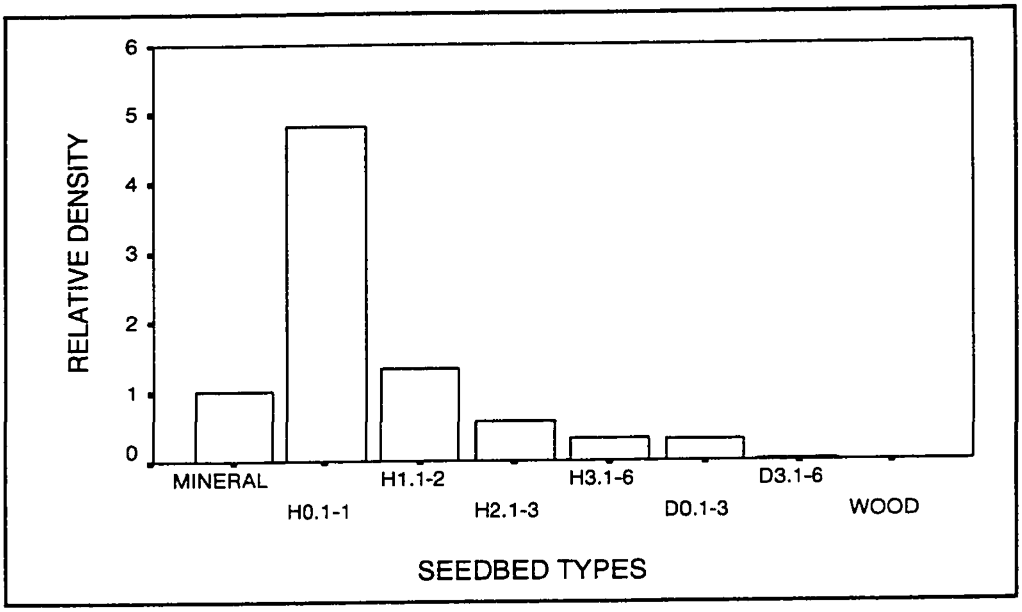
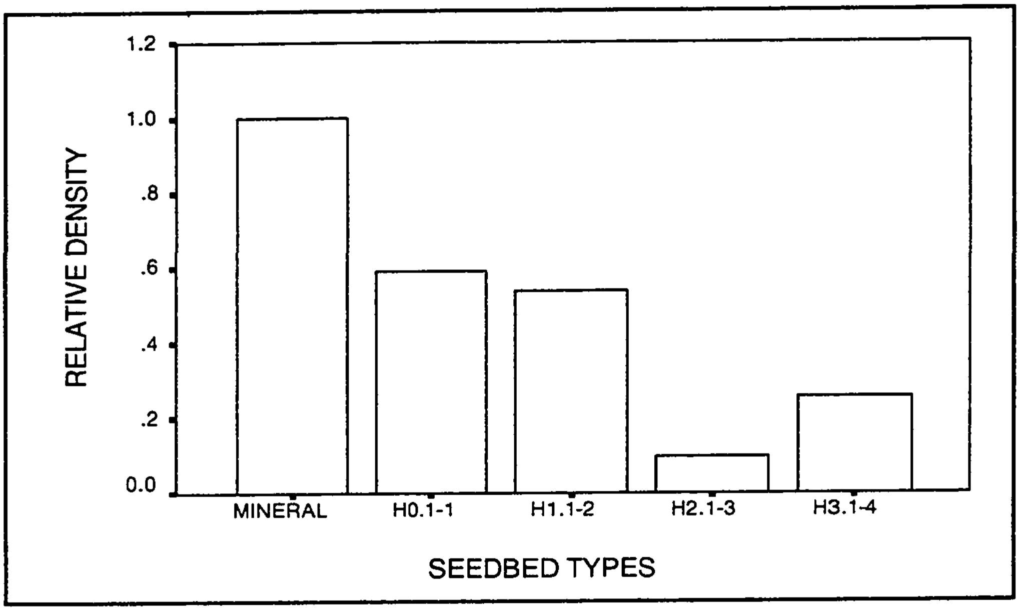
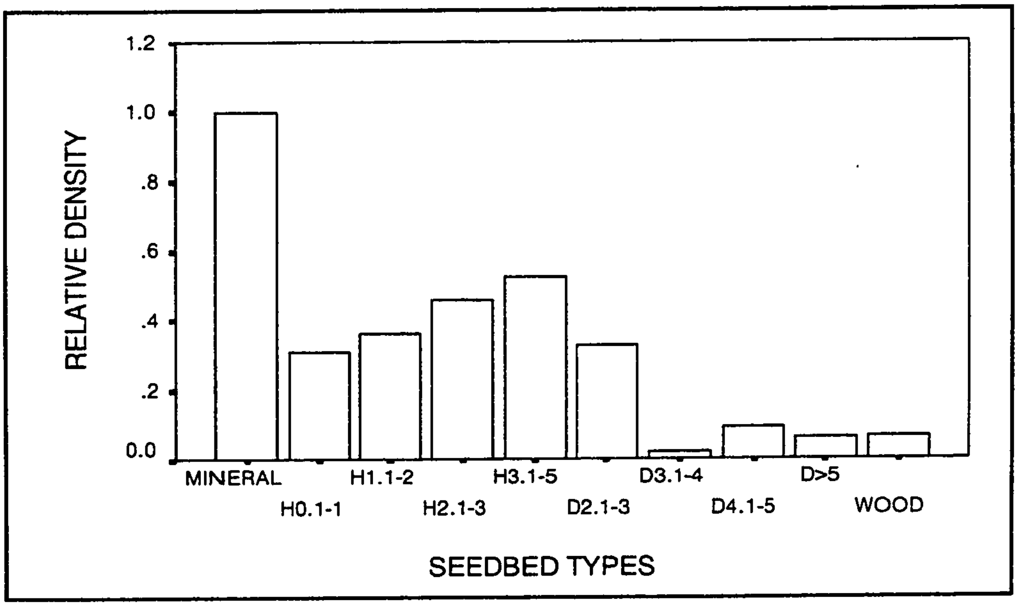


Figure 6. Relative densities of germinants on mineral soil, humus (H) and O_f (D) seedbeds (divided into depth classes), and decayed wood at Monday fire sites. Relative density is defined as the ratio of germinant density for a depth class over the germinant density on mineral soil.

a. Black spruce site



b. Jack pine site



c. Trembling aspen site

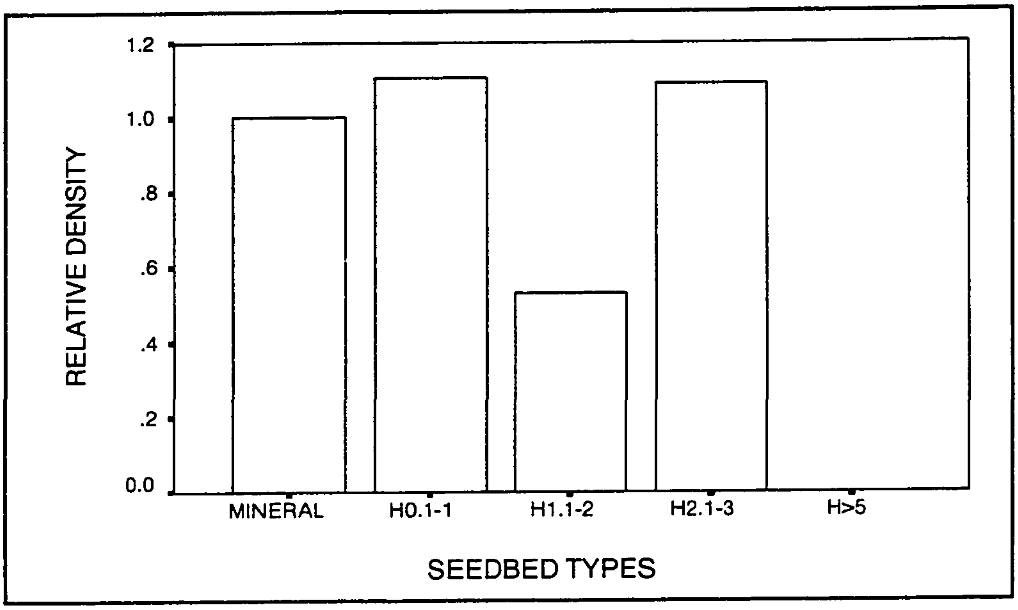


Figure 7. The relationship between relative density of germinants and organic layer depth. Crosses represent black spruce site in Bittern Creek fire, squares represent jack pine site in Bittern Creek fire, circles represent white spruce site in Bittern Creek fire, and triangles represent jack pine site in Monday fire.

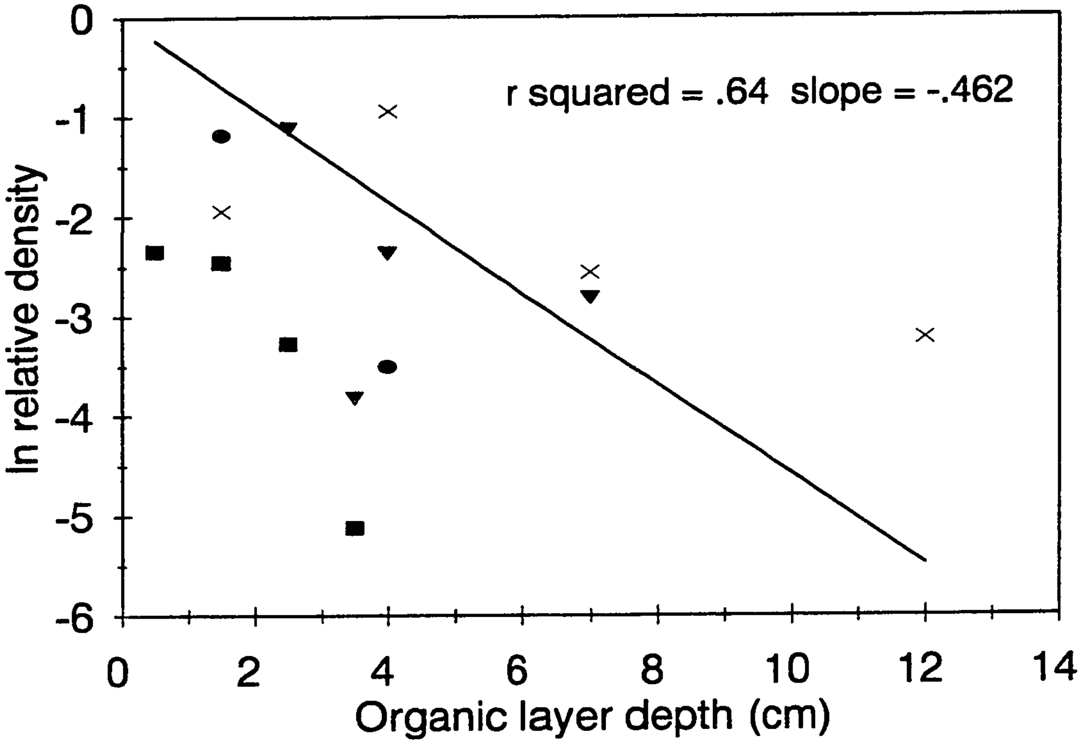
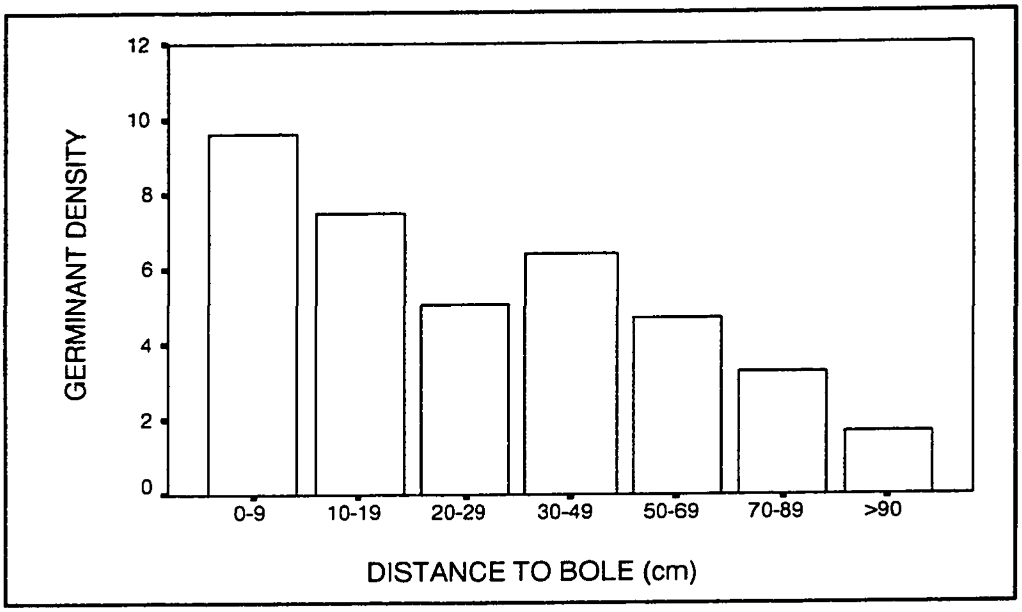
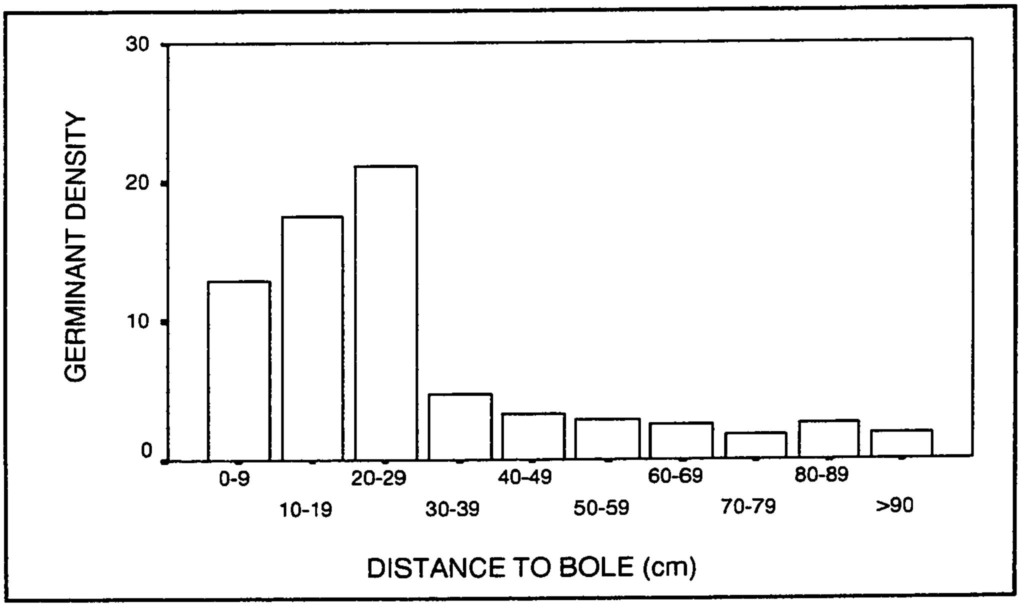


Figure 8. Density of germinants versus distance to nearest tree bole at Bittern Creek fire sites.

a. Black spruce site



b. Jack pine site



c. White spruce site

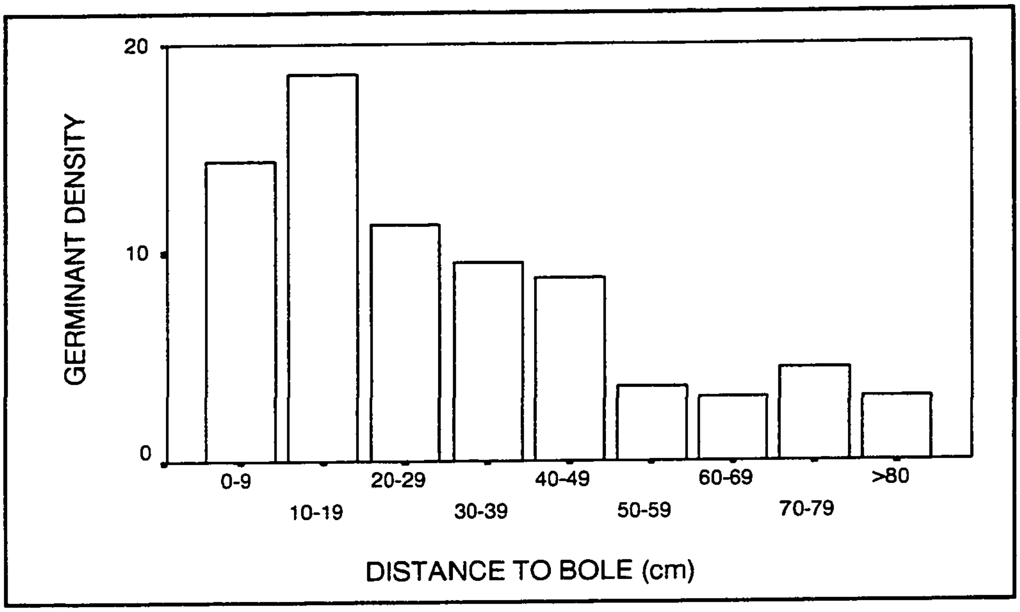
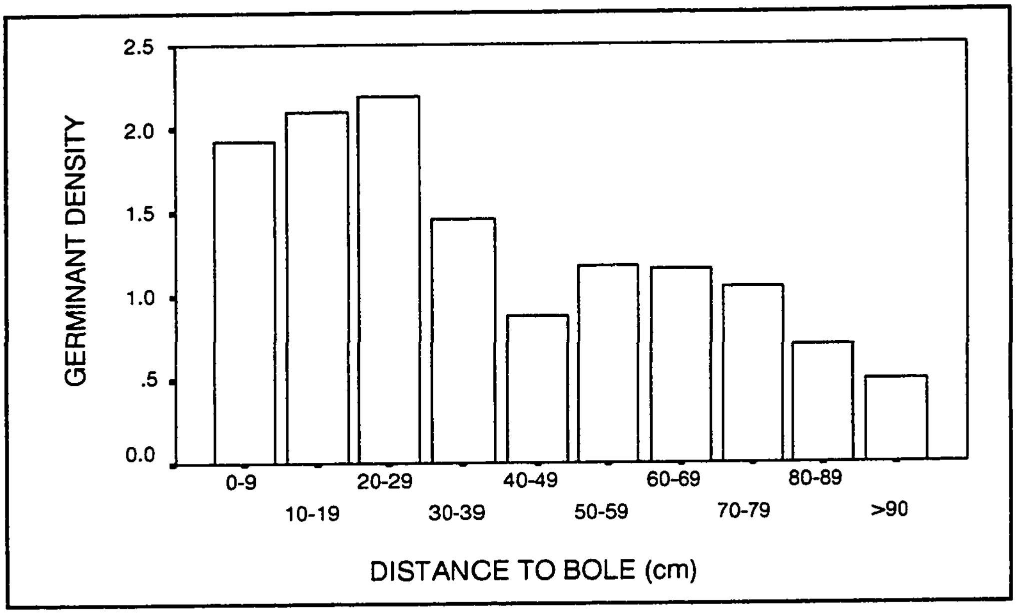
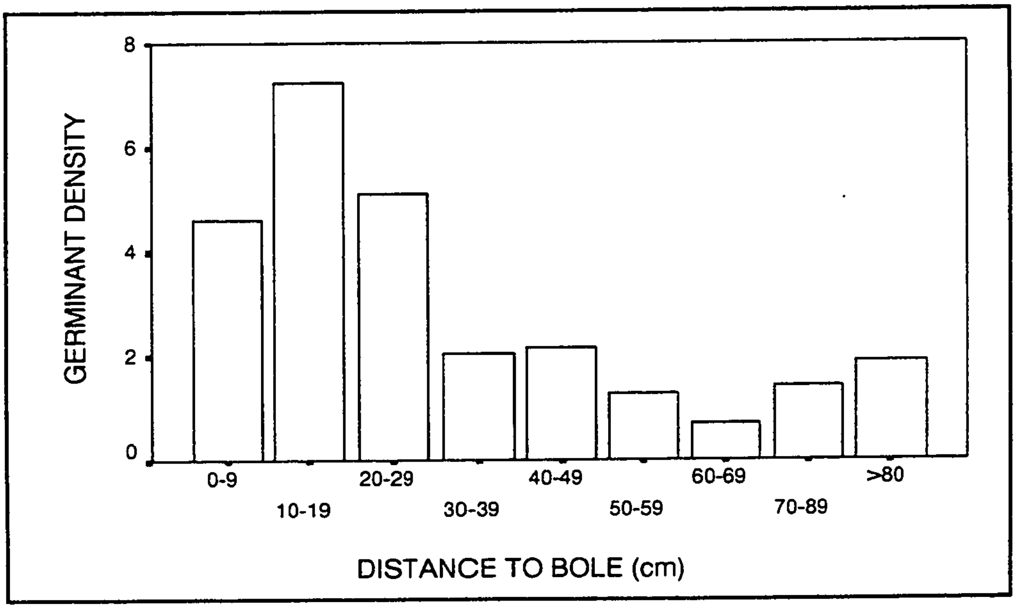


Figure 9. Density of germinants versus distance to nearest tree bole at Monday fire sites.

a. Black spruce site



b. Jack pine site



c. Trembling aspen site

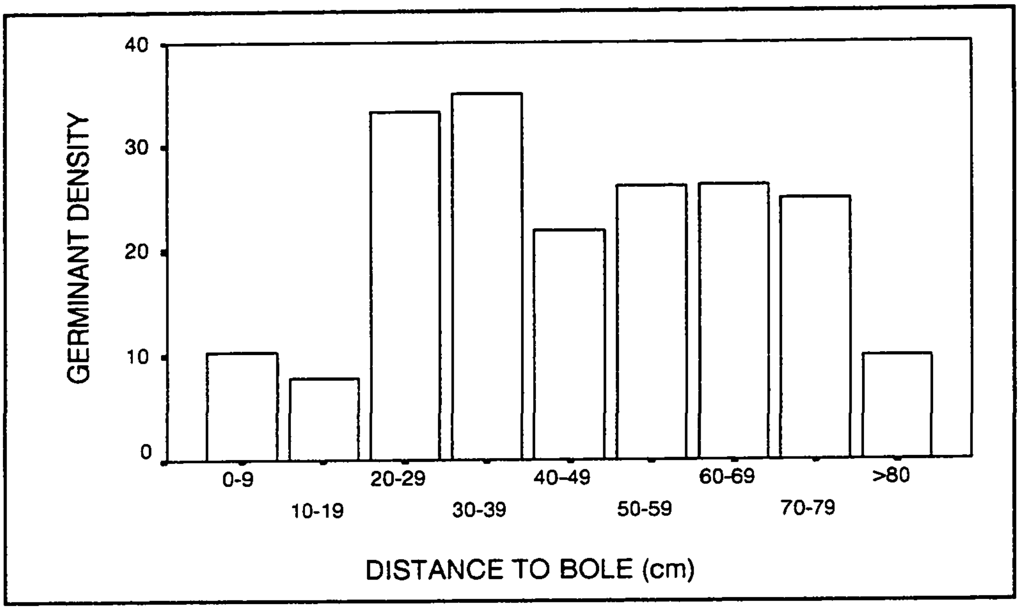
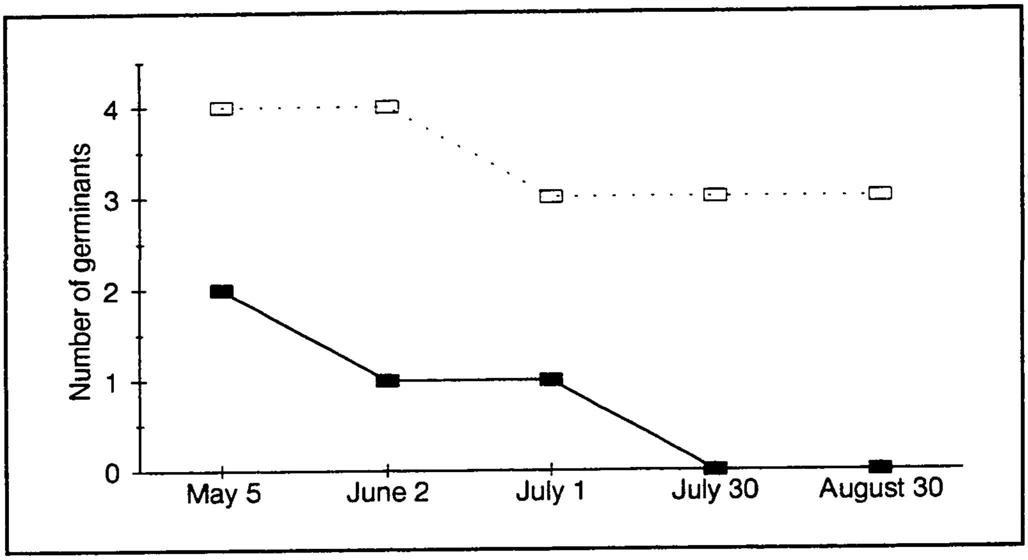


Figure 10. Number of 1996 cohort germinants at Bittern Creek fire sites. Open symbols represent mineral soil/humus seedbeds and filled symbols represent organic layer seedbeds. Squares represent jack pine and circles represent black spruce.

a. Black spruce site



b. Jack pine site

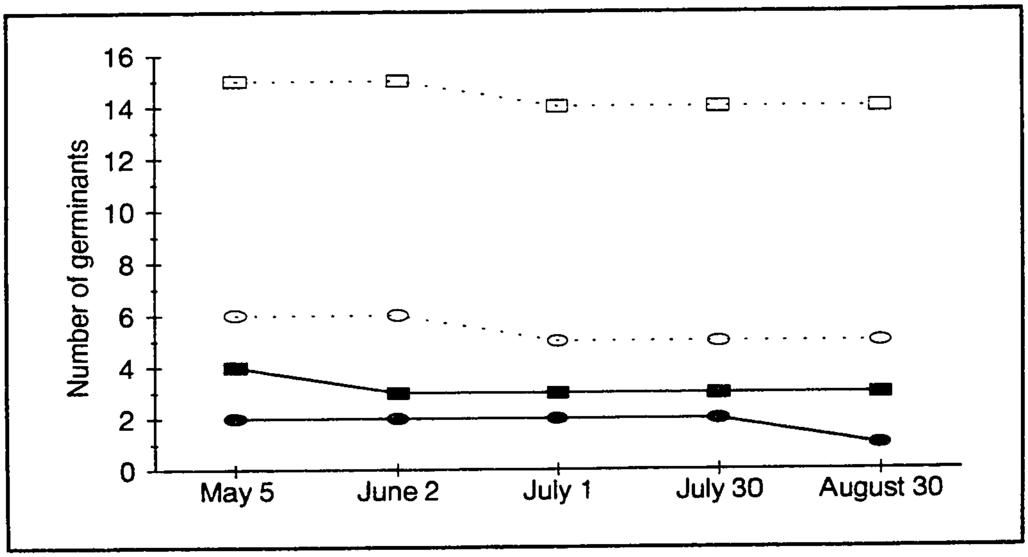
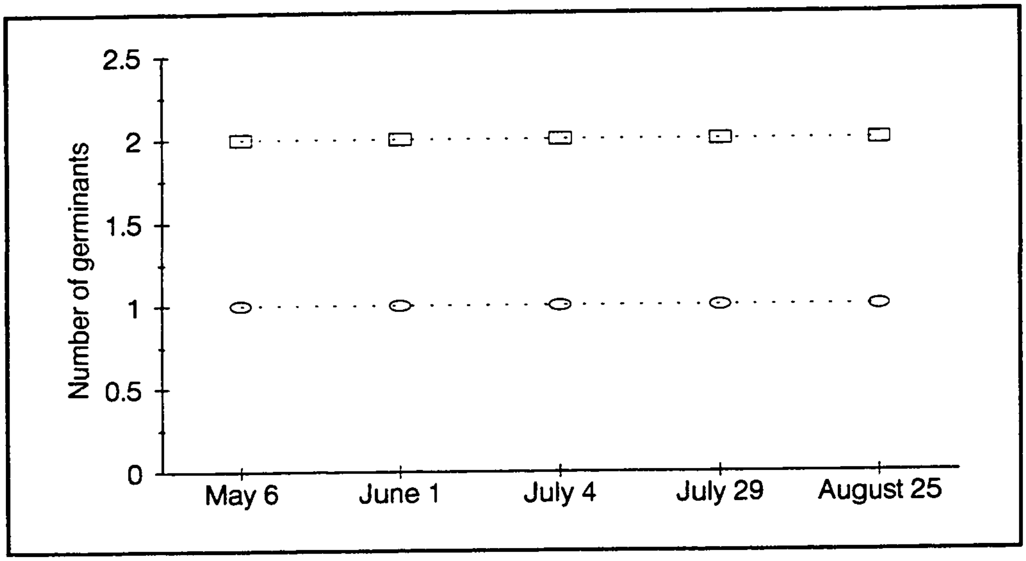


Figure 11. Number of 1995-1996 cohort germinants at Monday fire sites. Open symbols represent mineral soil/humus seedbeds and filled symbols represent organic layer seedbeds. Squares represent jack pine and circles represent black spruce.

a. Black spruce site



b. Jack pine site

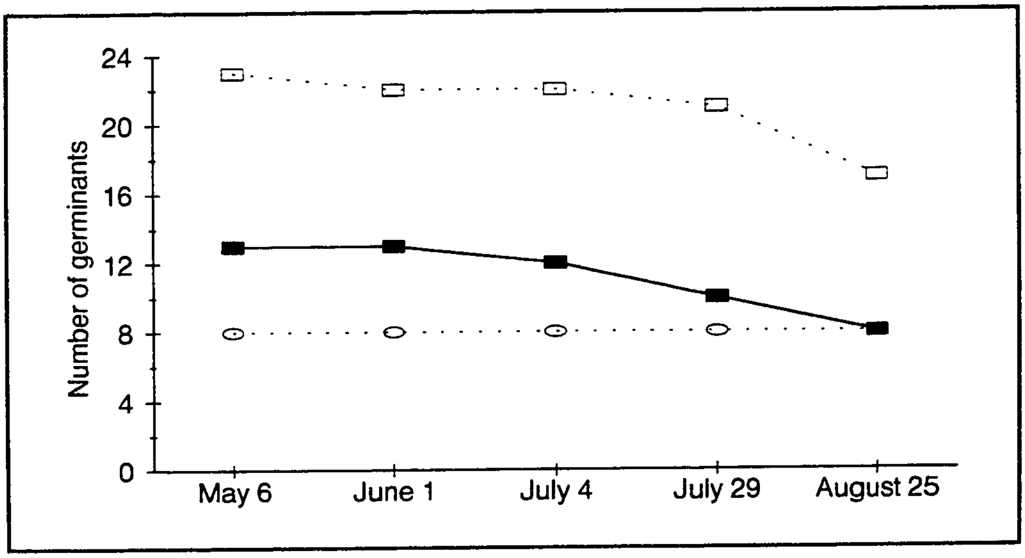
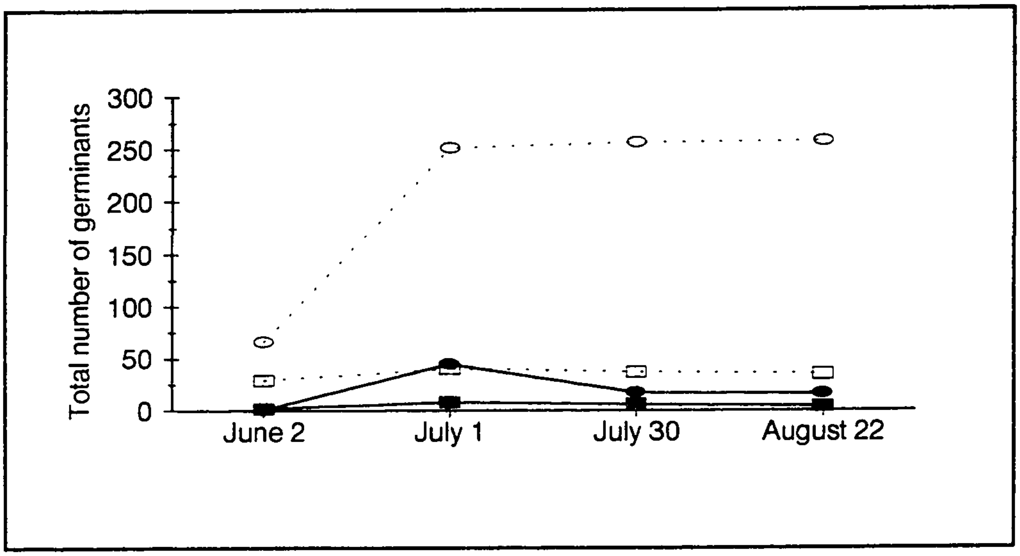
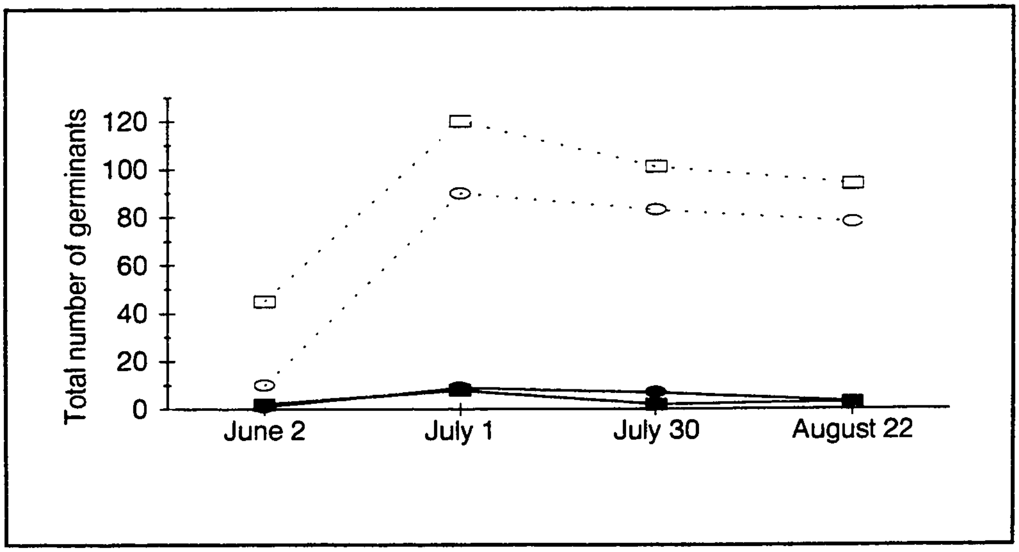


Figure 12. Cumulative number of 1997 cohort germinants at Bittern Creek fire sites. Open symbols represent mineral soil/humus seedbeds and filled symbols represent organic layer seedbeds. Squares represent jack pine, circles represent black spruce and triangles represent white spruce.

a. Black spruce site



b. Jack pine site



c. White spruce site

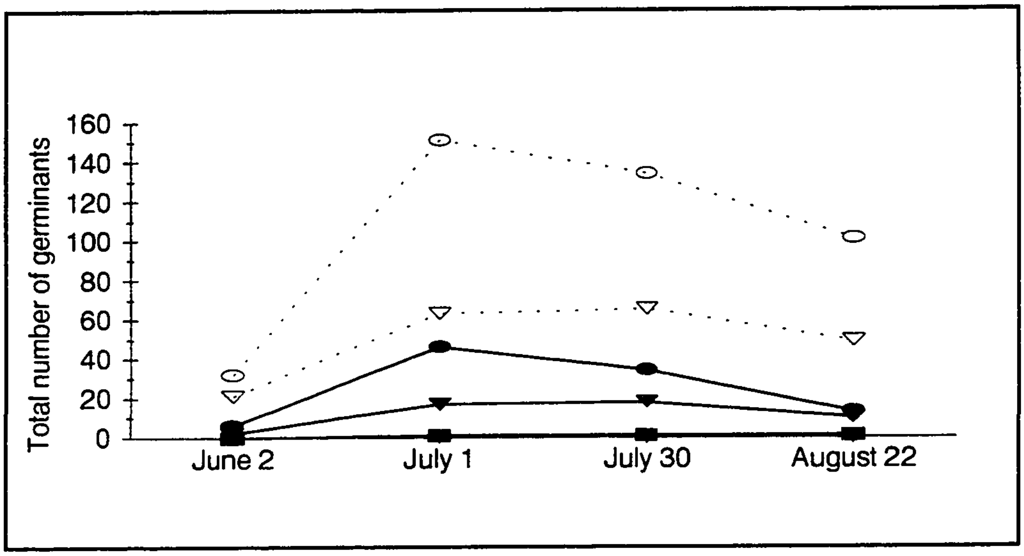
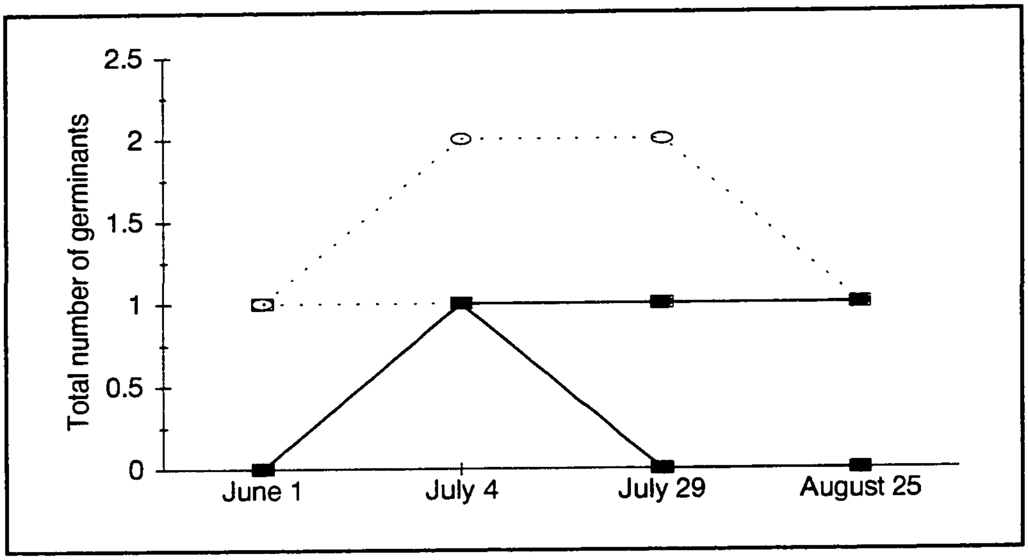


Figure 13. Cumulative number of 1997 cohort germinants at Monday fire sites. Open symbols represent mineral soil/humus seedbeds and filled symbols represent organic layer seedbeds. Squares represent jack pine and circles represent black spruce.

a. Black spruce site



b. Jack pine site

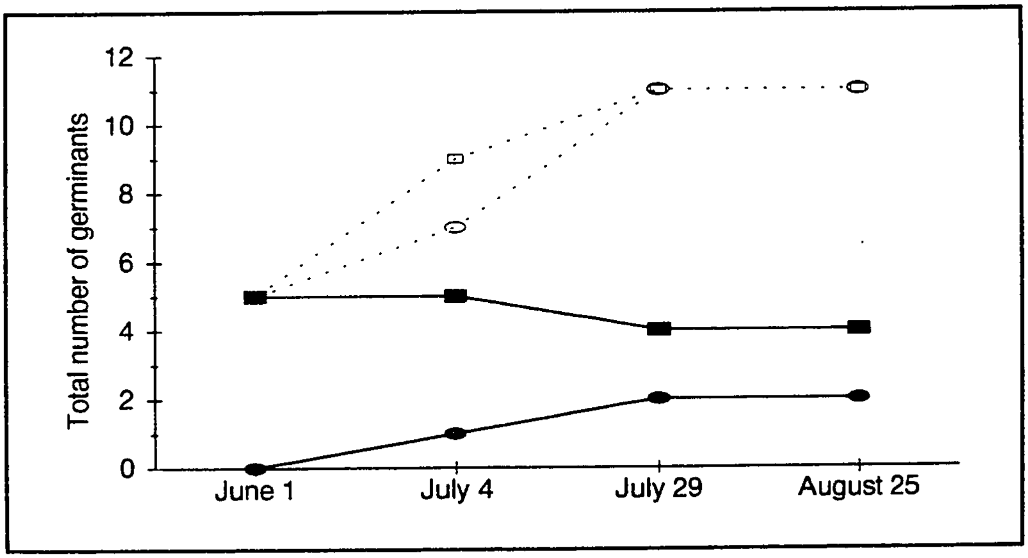
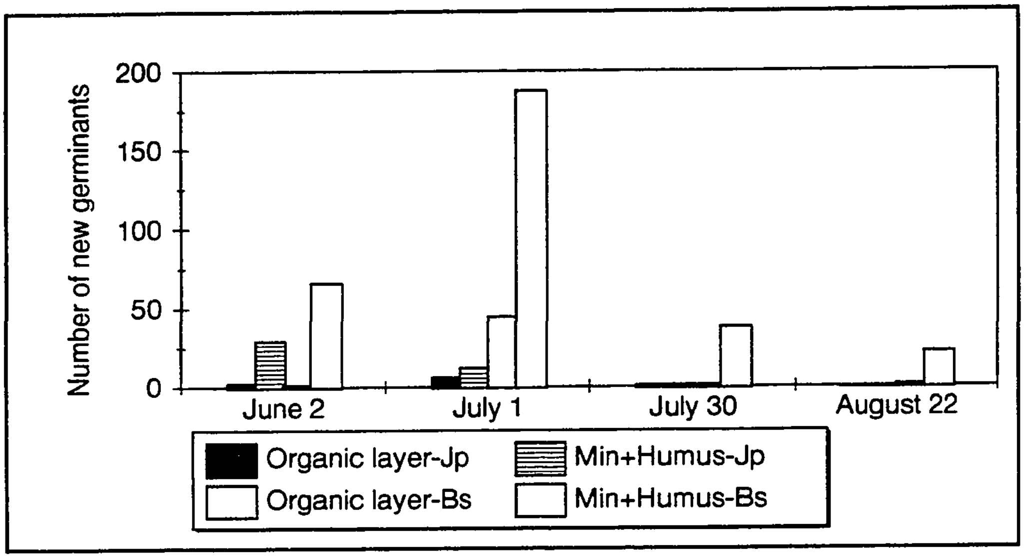
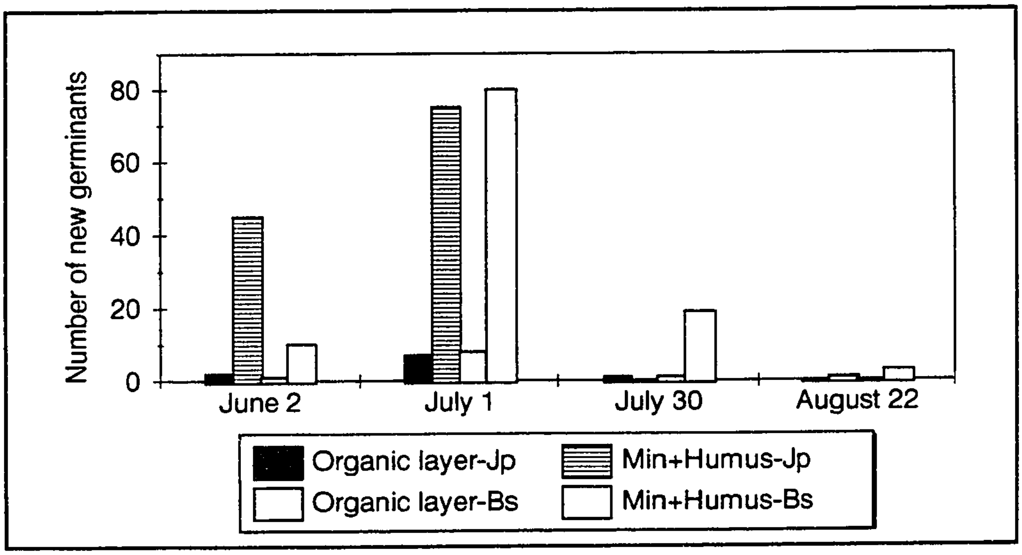


Figure 14. Number of new 1997 cohort germinants at Bittern Creek fire sites (Jp is jack pine, Bs is black spruce and Ws is white spruce).

a. Black spruce site



b. Jack pine site



c. White spruce site

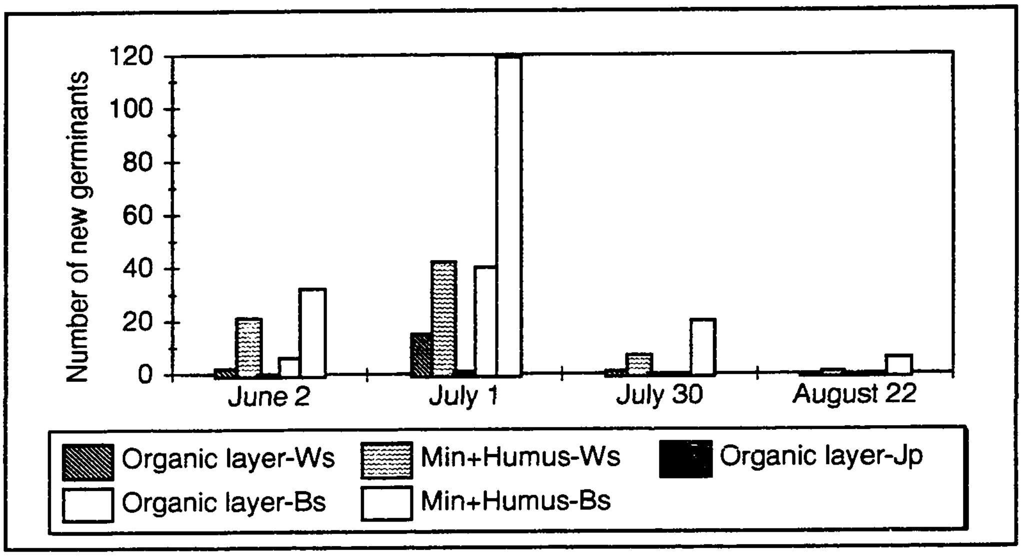
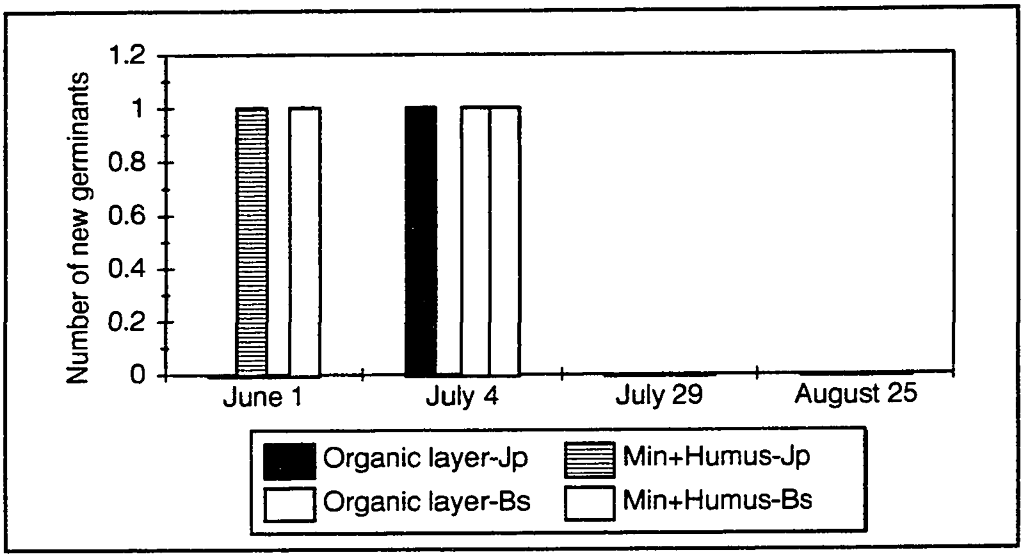


Figure 15. Number of new 1997 cohort germinants at Monday fire sites (Jp is jack pine, and Bs is black spruce).

a. Black spruce site



b. Jack pine site

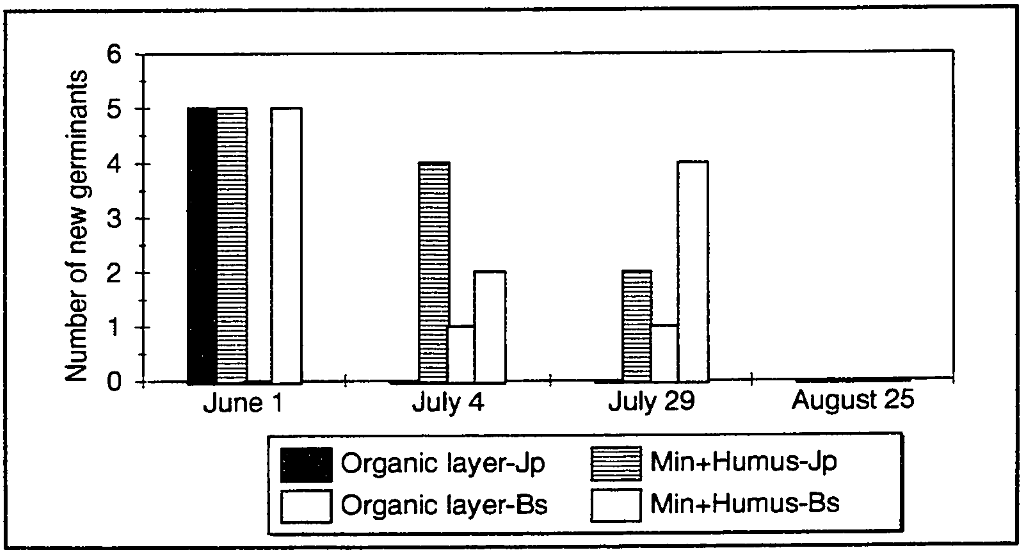


Figure 16. Percent survival of jack pine, black spruce and white spruce germinants of the 1997 cohorts on mineral soil/humus seedbeds at Bittern Creek fire sites (Jp is jack pine, Bs is black spruce and Ws is white spruce).

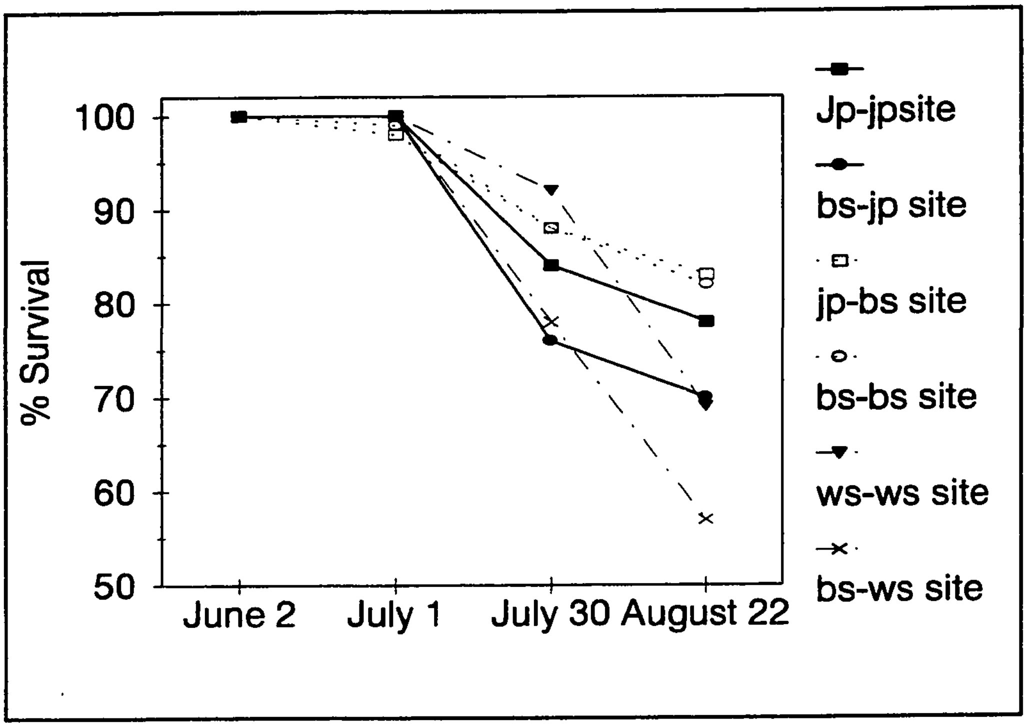
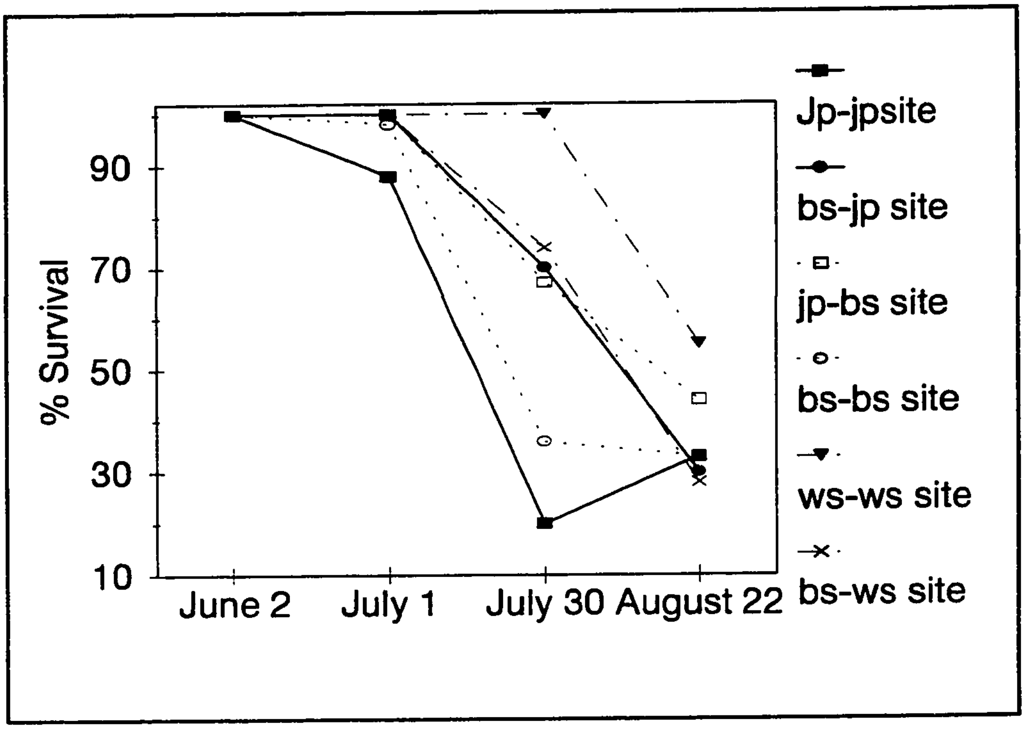


Figure 17. Percent survival of jack pine, black spruce and white spruce germinants of the 1997 cohorts on organic layer seedbeds at Bittern Creek fire sites (Jp is jack pine, Bs is black spruce and Ws is white spruce).



Appendices

Table A1. Seedbed depths for pot experiment (depths are in centimeters and are depths to mineral soil).

Species	Pot number	Depth of humus	Depth of burned moss (O_f)	Depth of humus + needles	Depth of humus + leaf
Jack pine	1	1.0	2.2	-	1.0
	2	0.6	2.5	-	0.4
	3	0.5	3.0	-	0.4
	Average	0.7	2.6	~0.5	0.6
Black spruce	1	0.3	4.5	-	0.5
	2	0.7	2.7	-	0.4
	3	0.5	2.8	-	0.2
	Average	0.5	3.3	~0.5	0.3
White spruce	1	0.4	3.0	-	0.3
	2	0.8	3.1	-	0.3
	3	0.4	3.5	-	0.2
	Average	0.5	3.2	~0.5	0.27

Table A2. ANOVA analysis for differences between germination values in pot experiment. Seedbeds are mineral soil, humus, burned moss (O_f), humus+needles and humus+leaf. Species are jack pine, black spruce and white spruce.

Source	**SS**	**df**	**F value**	**p value**
Seedbed	0.934	4	6.781	0.001
Species	0.081	2	1.181	0.321
Interaction	0.366	8	1.329	0.267

Table A3. ANOVA analysis for differences between survival values in pot experiment. Seedbeds are mineral soil, humus, burned moss (O_f), humus+needles and humus+leaf. Species are jack pine, black spruce and white spruce.

Source	SS	df	F value	p value
Seedbed	0.962	4	7.686	< 0.001
Species	0.288	2	4.595	0.018
Interaction	1.392	8	5.563	< 0.001

Table A4. Seedbed depths for field sowing experiment at Bittern Creek fire sites (values are in centimeters and are averages of three replicates).

Site	Seedbed type	Species sown	Depth to mineral	Depth of humus
Jack pine	Humus	Jack pine	0.6	0.6
		Black spruce	1.4	1.4
		White spruce	0.8	0.8
	Burned moss (O_f)	Jack pine	>20	-
		Black spruce	>20	-
		White spruce	>20	-
	Humus+Needles	Jack pine	0.8	0.8
		Black spruce	1.4	1.4
		White spruce	1.0	1.0
Black spruce	Humus	Jack pine	0.9	0.9
		Black spruce	1.1	1.1
		White spruce	0.9	0.9
	Burned moss (O_f)	Jack pine	>20	-
		Black spruce	>20	-
		White spruce	>20	-
	Humus+Needles	Jack pine	1.1	1.1
		Black spruce	4.1	4.1
		White spruce	0.5	0.5
White spruce	Humus+Needles	Jack pine	0.1	0.1
		Black spruce	0.4	0.4
		White spruce	0.6	0.6

Table A5. Seedbed depths for field sowing experiment at Monday fire sites (values are in centimeters and are averages of three replicates).

Site	Seedbed type	Species sown	Depth to mineral	Depth of humus	Seedbed depth
Jack pine	Humus	Jack pine	1.3	1.3	1.3
		Black spruce	1.3	1.3	1.3
		White spruce	1.8	1.8	1.8
	M. polymorpha	Jack pine	1.5	1.5	-
		Black spruce	1.4	1.4	-
		White spruce	1.8	1.8	-
	P. juniperinum	Jack pine	3.6	1.0	2.6
		Black spruce	3.4	0.8	2.5
		White spruce	4.7	1.4	3.3
Black spruce	Humus	Jack pine	1.1	1.1	1.1
		Black spruce	2.0	2.0	2.0
		White spruce	2.3	2.3	2.3
	M. polymorpha	Jack pine	1.6	1.6	-
		Black spruce	1.4	1.4	-
		White spruce	1.1	1.1	-
	P. juniperinum	Jack pine	4.3	1.6	2.7
		Black spruce	5.7	2.9	2.8
		White spruce	4.4	1.9	2.5

Table A6. Seedbed depths for field sowing experiment at Muskeg fire sites (values are in centimeters and are averages of three replicates).

Site	Seedbed type	Species sown	Depth to mineral	Depth of humus	Seedbed depth
Jack pine	Aspen litter	Jack pine	2.5	0.6	1.9
		Black spruce	3.9	2.4	1.5
		White spruce	1.8	1.5	0.3
Black spruce	Aspen litter	Jack pine	2.2	1.7	0.5
		Black spruce	1.7	1.4	0.3
		White spruce	2.5	2.1	0.4
White spruce	*P. juniperinum*	Jack pine	6.0	1.5	4.5
		Black spruce	5.8	1	4.7
		White spruce	9.9	1.4	24.4

Table A7. ANOVA analysis for difference between germination values of field sowing experiment at Bittern Creek fire sites. Seedbeds are mineral soil, humus, burned moss (O_f) and humus+needles. Species are jack pine, black spruce and white spruce.

Site	Source	SS	df	F value	p value
Black spruce	Seedbed	0.692	3	7.574	0.001
	Species	0.430	2	7.068	0.004
	Interaction	0.776	6	4.250	0.005
Jack pine	Seedbed	1.242	3	21.457	< 0.001
	Species	0.099	2	2.559	0.098
	Interaction	0.208	6	1.795	0.143
White spruce	Species	0.270	2	1.795	0.245

Table A8. ANOVA analysis for differences between germination values of field sowing experiment at Monday fire sites. Seedbeds are humus, *P. juniperinum* and *M. polymorpha*. Species are jack pine, black spruce and white spruce.

Site	Source	SS	df	F value	p value
Black spruce	Seedbed	0.293	2	6.189	0.009
	Species	0.227	2	4.974	0.021
	Interaction	0.257	4	2.714	0.063
Jack pine	Seedbed	0.080	2	1.718	0.208
	Species	0.108	2	2.313	0.128
	Interaction	0.214	4	2.302	0.098

Table A9. ANOVA analysis for differences between germination values of field sowing experiment at Muskeg fire sites. Seedbeds are *P. juniperinum* and aspen leaf litter. Species are jack pine, black spruce and white spruce.

Site	Source	SS	df	F value	p value
Black spruce	Seedbed	0.312	2	8.903	0.011
	Species	0.282	1	4.026	0.046
	Interaction	0.119	2	1.7004	0.223
Jack pine	Species	0.005	2	0.506	0.626

Table A10. ANOVA analysis for differences between survival values of field sowing experiment at Bittern Creek fire sites. Seedbeds are mineral soil, humus, burned moss (O_f) and humus+needles. Species are jack pine, black spruce and white spruce.

Site	Source	SS	df	F value	p value
Black spruce	Seedbed	4.014	3	19.993	< 0.001
	Species	0.099	2	0.741	0.487
	Interaction	0.314	6	0.782	0.592
Jack pine	Seedbed	4.409	3	32.934	< 0.001
	Species	0.353	2	3.950	0.033
	Interaction	0.674	6	2.519	0.049
White spruce	Species	0.293	2	2.345	0.177

Table A11. ANOVA analysis for differences between survival values of field sowing experiment at Monday fire sites. Seedbeds are humus, *P. juniperinum* and *M. polymorpha*. Species are jack pine, black spruce and white spruce.

Site	Source	SS	df	F value	p value
Black spruce	Seedbed	0.093	2	0.893	0.427
	Species	0.098	2	0.938	0.410
	Interaction	0.164	4	0.784	0.551
Jack pine	Seedbed	0.649	2	1.364	0.281
	Species	0.095	2	0.200	0.821
	Interaction	0.264	4	0.277	0.889

Table A12. ANOVA analysis for differences between survival values of field sowing experiment at Muskeg fire sites. Seedbeds are *P. juniperinum* and aspen leaf litter. Species are jack pine, black spruce and white spruce.

Site	Source	SS	df	F value	p value
Black spruce	Seedbed	3.516	2	217.608	< 0.001
	Species	0.121	1	3.750	0.054
	Interaction	0.121	2	3.750	0.054
Jack pine	Species	0.056	2	1.0	0.422