FOREST FLOOR SEED BANKS AND THEIR RESPONSE TO SLASHBURNING IN SOME FOREST ECOSYSTEMS IN SOUTH CENTRAL BRITISH COLUMBIA

By

H. KAREN YEARSLEY

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ABSTRACT

Soil seed banks are part of the flora of many ecosystems, but little is known about those of temperate coniferous forests in B.C., or their response to different disturbances. As a result, a study of forest floor seed banks and their response to the common disturbances of clearcutting and slashburning, was conducted in the Engelmann Spruce - Subalpine Fir (ESSF) and Interior Cedar - Hemlock (ICH) biogeoclimatic zones of south central B.C. Studies were carried out on the Devil's Club - Lady fern sites series in the ESSFwc2 variant and on the Oak fern site series in the ICHwk1 variant in the Clearwater Forest District.

The species composition, numbers and distribution of seeds were determined through greenhouse germination of forest floor samples split into 1 cm layers. Germinant density was 2591/m^2 and 689/m^2 in the ESSF and ICH samples, respectively. Most germinants (82 and 92% in the ESSF and ICH, respectively) belonged to the five most abundant taxa from each site and most (78 and 97% in the ESSF and ICH, respectively) were present in the top 3 cm of the forest floor. Seeds were poorly dispersed among the samples and highly clustered in the samples in which they occurred. Germinants of most taxa decreased with depth, but other distributions were found. Vertical distribution patterns varied widely among samples.

Germination from the seed bank in both unburned and burned areas on the study sites showed that 1) germinant density was much lower in the field than in the greenhouse samples, and 2) burned areas had many fewer germinants than did unburned areas on the ESSF site, but the reverse was found on the ICH site.

Soil temperatures were measured during and after slashburning on the study sites. Forest floor depth of burn was also measured, and no relationship could be demonstrated between depth of burn and soil temperatures during burning. Therefore, the effect of elevated temperatures on buried seeds could not be determined.

Shading reduced post-burn soil temperatures on both sites, but the influence of these temperatures on germination was not clear due to inconsistent results and lack of replication. Burning significantly reduced germination, whereas shading resulted in significantly more germinants in burned, but not unburned, areas of the ESSF site. The effect of shading and burning on germination on the ICH site could not be determined due to a lack of germinants.

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CHAPTER 1 GENERAL INTRODUCTION

A soil seed bank consists of all viable seeds (dormant but capable of germination) found within the soil profile including the surface organic horizons ('forest floor'). Soil seed banks have been found in nearly all plant communities that have been studied. Buried seeds occur in arctic, tropical, grassland, desert and wetland ecosystems, and in cultivated land and soil undisturbed for hundreds of years. As such, seeds are an important part of the species composition of plant communities, but one that is often overlooked when inventories of diversity are made. This oversight may be partly because some species are present only as buried seeds at certain stages of a plant community's development. Therefore, geographical distribution of species should also include seed banks to be complete.

Germination of seeds from seed banks is an important source of new plants in many of these communities. In order for germination to take place, however, some alteration in the seed environment is usually required. Disturbance can change temperature, moisture, light or chemical conditions in the soil such that seeds overcome dormancy and germinate.

Depending on the size and severity, disturbance can also initiate secondary succession in plant communities. Thus, germination of buried seeds can be an important means of revegetation after disturbance. Understanding plant succession must, therefore, include the study of seed banks and their response to disturbance.

Buried seeds are also present in forest soils including

those of northern temperate and boreal forests. As pressures on forest land increase, there is a need to learn about the biodiversity (genetic, species, structural and temporal) of old-growth forests. Management activities for whatever purpose (forestry, wildlife, parks, mining) cause disturbances in forests. Information on the impact of such disturbances on succession and natural diversity is required in order to minimize damage to forest ecosystems and to aid in reconstruction of damaged areas. Seed banks may be as important for conserving genetic and species diversity over time as other sources of new plants. Maintaining biodiversity therefore includes an understanding of how to maintain seed banks.

As one of the most important economic activities in B.C., logging, and subsequent site preparation and stand tending, is probably the single largest source of disturbance in B.C.'s forests. While vegetative regeneration and germination from off-site seeds (*e.g.* fireweed) are both commonly observed after clearcutting, little is known about the composition of, or germination from, seed banks of forest soils in British Columbia or Canada. Neither the long-term contribution of seed banks to forest vegetation over time, nor the means by which seed banks are maintained, are well known for this province.

In managed forests with a dense closed canopy, many of the non-crop plant species that contributed to the natural diversity of the original forest, may die out over the rotation, leaving seed banks as possibly the only source of propagules on the site. Even in second growth stands that are spaced and thinned, there may be few plants left to reproduce either vegetatively or by

seeds. However, without a knowledge of species-specific seed longevity, the type and severity of disturbance required to stimulate germination or the means by which seed banks are maintained in forests, it cannot be assumed that seed banks will supply the wildlife forage, and species and structural diversity presently lacking in some managed forest plantations.

In south central B.C. forests have high economic and biodiversity values for timber harvesting, recreational activities and wildlife habitat. Timber harvesting typically involves clearcutting followed by slashburning. In view of the importance of these values and the lack of knowledge about seed banks and their response to disturbances such as logging and site preparation, the present study was established with the objective of quantifying forest soil seed banks and their response to clearcutting and slashburning in important forest zones in this area. This information should also provide a basis for further studies that specifically address long-term succession and the characterization and maintenance of biological diversity.

CHAPTER 2 THE SEED BANK

2.1 Introduction

Studies of temperate forest soils in other areas of North America and Europe have found varying numbers of seeds. Germination of seeds stored in the soil is an important mode of revegetation for some of these forest communities (Marks 1974; Bormann and Likens 1979; Heinselman 1981). Only two studies conducted in B.C. have been published (Kellman 1970, 1974) and these concern coastal forests. Another study of disturbed coastal forest soils was carried out as part of a PhD thesis (McGee 1988). In the interior of the province, studies have been done in the Sub-Boreal Spruce Zone (Hamilton & Yearsley unpublished data). When the present study was initiated, there was no information on seed banks in the Engelmann Spruce Subalpine Fir (ESSF) and Interior Cedar Hemlock (ICH) biogeoclimatic zones (Pojar *et al.* 1987) where timber harvesting is important.

Before the role of seed banks in revegetation after either natural or human-caused disturbances can be determined, baseline data on species composition, abundance and distribution of viable seeds in the soil is needed. Species composition of the seed bank may provide information about vegetation history, and a basis for predicting post-disturbance plant communities and distribution. Seed abundance might be related to species importance in the some post-disturbance communities, and to species-specific productivity. We know little or nothing about the relationship between plant and seed distribution. The horizontal distribution of seeds may provide information about dispersal and seed burial

patterns and possibly the distribution of the source plants. Vertical seed distribution is important to predict the response of seeds to depth-dependant disturbances such as fire.

Few studies have attempted to determine the distribution of seeds. In many studies variability among samples, which is a broad indication of horizontal distribution, has been deliberately eliminated by mixing samples together and then assessing subsamples. Where vertical distribution of seeds has been reported, samples have been split into very few layers and/or layers that were too thick to allow for detailed resolution of vertical patterns.

Most seed bank studies have either counted and identified germinants that emerged from soil samples in a greenhouse, or extracted, identified and tested the viability of seeds from soil samples (Roberts 1981). While both methods are useful, neither provide information about what species actually germinate from soil in the field. This is perhaps as significant to revegetation as determining the exact species composition and abundance of buried seeds. None of the coniferous forest studies has adequately examined germination in the field, attempted to measure field conditions that might influence germination from seed banks or compared field with greenhouse germination conditions.

The specific objectives of this part of the study were to quantify the species composition, abundance and distribution of seeds in some forest floors in the ICH and ESSF zones in south central British Columbia. Two approaches were taken to collecting information to describe the seed banks of the areas studied.

First, forest floor samples were collected from the site, split into layers and monitored for germinants in a greenhouse. The second approach was to monitor germination on the same site in the field. The greenhouse germination yielded information on vertical and horizontal seed distribution, while the field germination provided a comparison with the artificial greenhouse environment, and between unburned and burned forest floor (see Chapter 3).

2.2 Methods

2.2.1 Study design and layout

Intensive studies were carried out on two cutblocks located in the Clearwater Forest District (Figure 2.1), that were logged during the winter of 1988/1989 and operationally slashburned in the fall of 1989. Unburned control areas were retained in both study blocks. The sites were selected for minimum forest floor disturbance and a relatively uniform topography.

One site was located in the Northern Monashee Wet Cold variant of the Engelmann Spruce-Subalpine Fir biogeoclimatic zone (ESSFwc2). This site was identified as the Devil's club - Lady fern site series (07) (Lloyd *et al.* 1990), with a well-developed understory of herbs such as *Valeriana sitchensis*, *Athyrium filix-femina*, *Gymnocarpium dryopteris* and *Tiarella unifoliata*, shrubs dominated by *Rhododendron albiflorum*, *Menziesia ferruginea*, *Vaccinium membranaceum* and *V. ovalifolium*, and a sparse moss layer. Characteristics of the site also included a moderate slope gradient, southeast aspect, with a moist (subhygric) soil moisture regime and a rich (permesotrophic) soil nutrient regime.

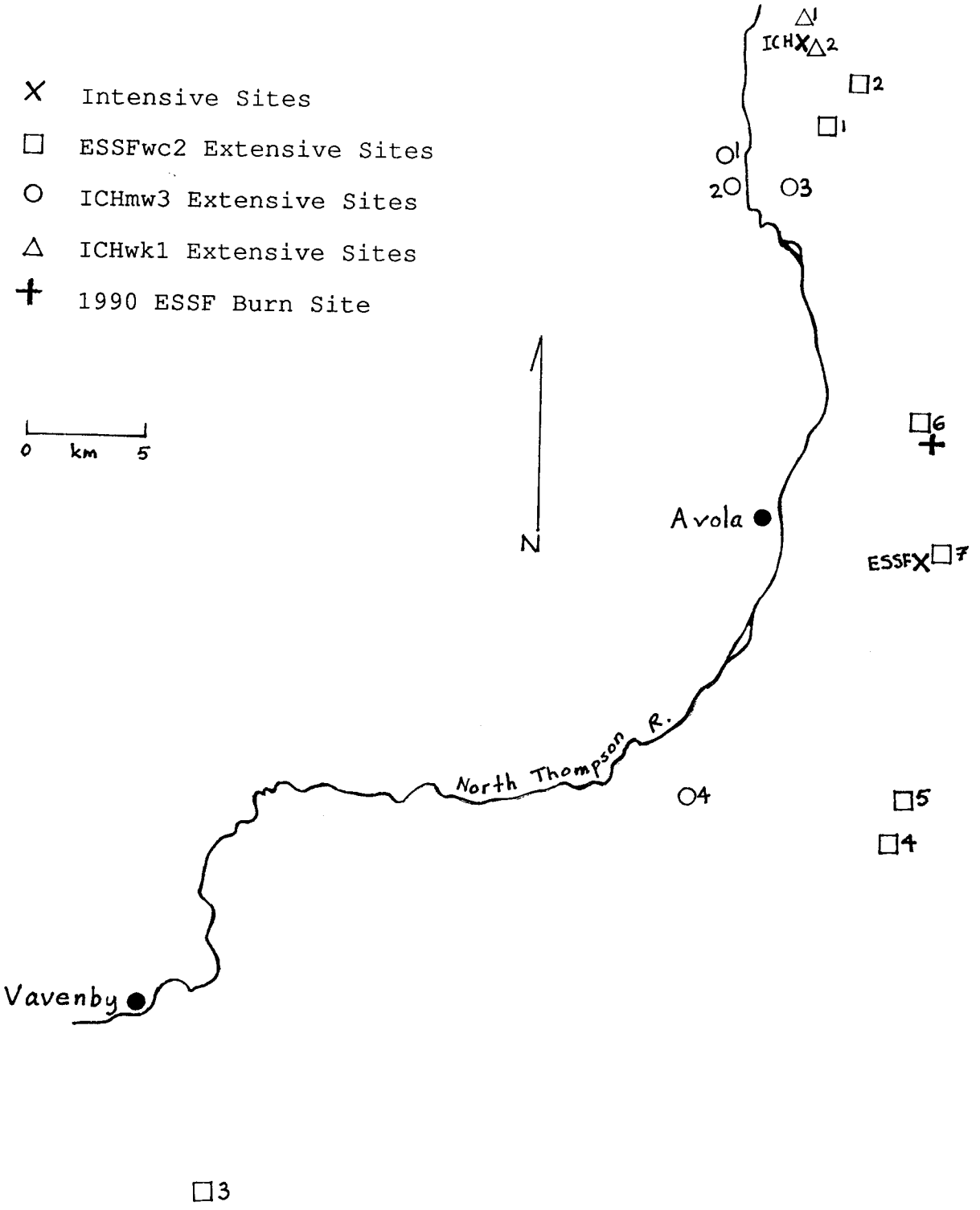

Figure 2.1 Location of the intensive and extensive study sites. Numbers beside symbols correspond to site numbers.

The site was located at km 30 on the Otter Ck. Forest Service Road approximately 50 km north of Clearwater.

The other site was in the Wells Gray Wet Cool variant of the Interior Cedar-Hemlock biogeoclimatic zone (ICHwk1) (Pojar *et al.* 1987). This site was identified as the zonal Oak fern site series (01) (Pojar *et al.* 1987; Lloyd *et al.* 1990), and had a sparse understory of herbs, including *Gymnocarpium dryopteris*, *Tiarella unifoliata*, *Clintonia uniflora* and *Cornus canadensis*, shrubs such as *Vaccinium membranaceum* and *V. ovalifolium*, and a 1 - 2 cm thick layer of mosses. Characteristics of the site also included a gentle slope, southwest aspect, and intermediate soil moisture (mesic) and nutrient (mesotrophic) regimes. The site waslocated at km 7.5 on the South Foam Ck. Forest Service Road about 80 km north of Clearwater. The humus forms found on both the ESSF and ICH sites were hemimors and hemihumimors (Klinka *et al.* 1981, Lloyd *et al.* 1990).

On each intensive site, 12 - 3 X 3 m plots were established. Nine plots were located in an area to be burned while the other three plots were located in an unburned control area. In each plot, 25 - 10 X 10 cm subplots were established at grid points spaced 0.5 m apart each way (Figure 2.2). Subplots were offset only where there were stumps or large logs resting on the ground at the grid points. Forest floor samples were collected in the undisturbed forest floor close to the plots, using the same grid pattern as the subplots (Figure 2.2).

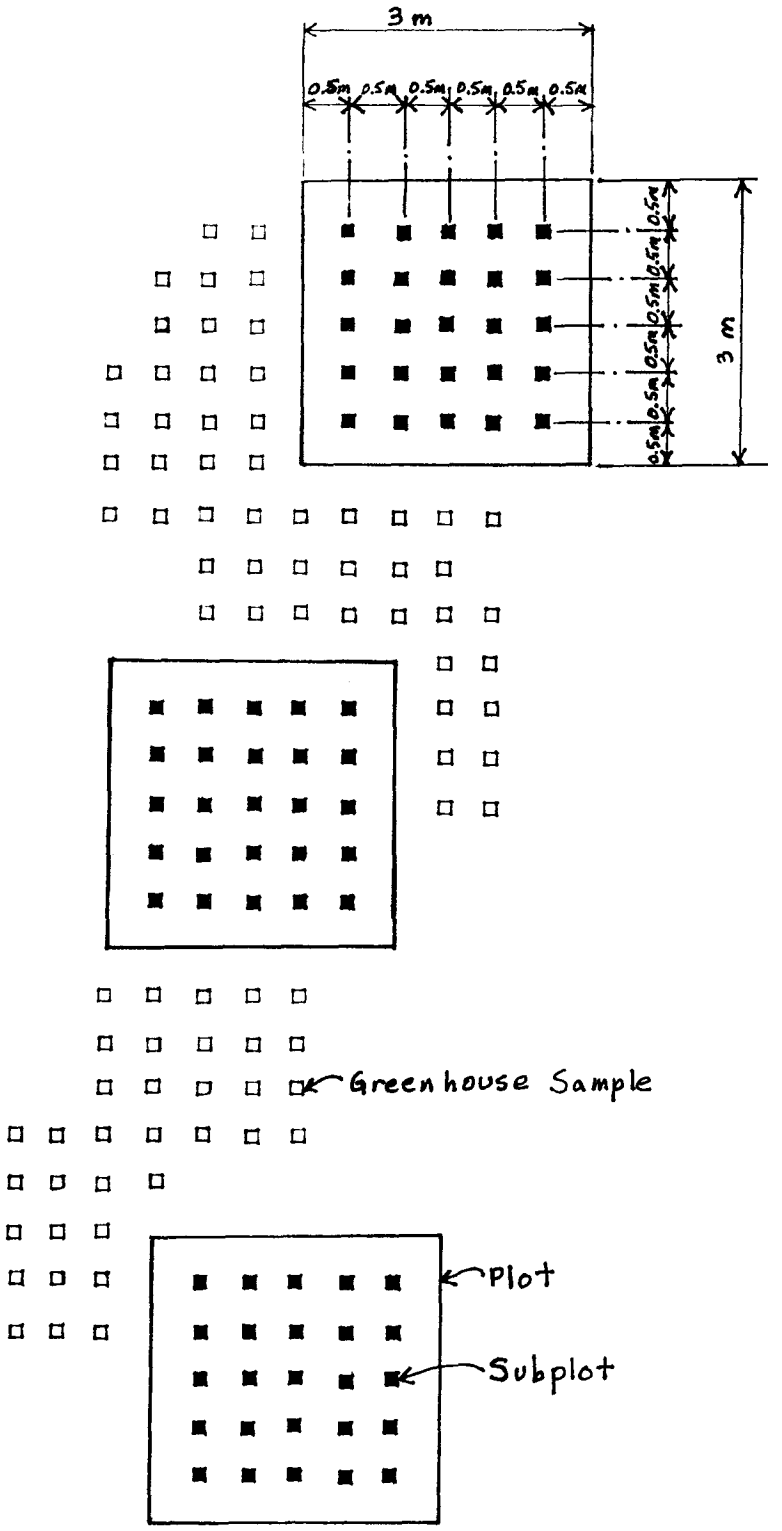

Figure 2.2 Schematic layout of plot, subplot and greenhouse sample locations in the ESSF and ICH field sites. (Not all plots are shown.)

2.2.2 **Greenhouse germination**

2.2.2.1 Data collection

Three-hundred and four - 10 X 10 cm forest floor (LFH) samples were collected from each intensive site before burning. Other studies of temperate coniferous forest seed banks have generally shown very few seeds in mineral soil (Moore and Wein 1977; Graber and Thompson 1978; Granstrom 1982) so only the organic layers were sampled. Samples were collected in July, 1989.

During the collection period, samples were kept outside covered with remay cloth to exclude seed rain. Once all samples from a site had been collected, they were transported to the University of B.C. and stored in a refrigerated room at approximately 4^{o}C. When stacking was necessary during transport and storage, layers of remay were placed between samples to prevent contamination, and inverted greenhouse trays were used as spacers to prevent compression of samples.

In October 1989, the samples were removed from the refrigerated room and taken to the Saanich Peninsula where they were covered and stored outside for about two weeks, then moved into an unheated, plastic-covered greenhouse.

Many of the ICH samples had a thick moss layer which was trimmed off and discarded. Although seeds may have been lost along with this moss, none were observed and any that were there probably originated from recent seed rain. The moss on the ESSF samples was thin or absent and was therefore left intact. Each sample was split parallel to the soil surface into 1 cm layers (Figure 2.3). Layers were placed in individual square containers,

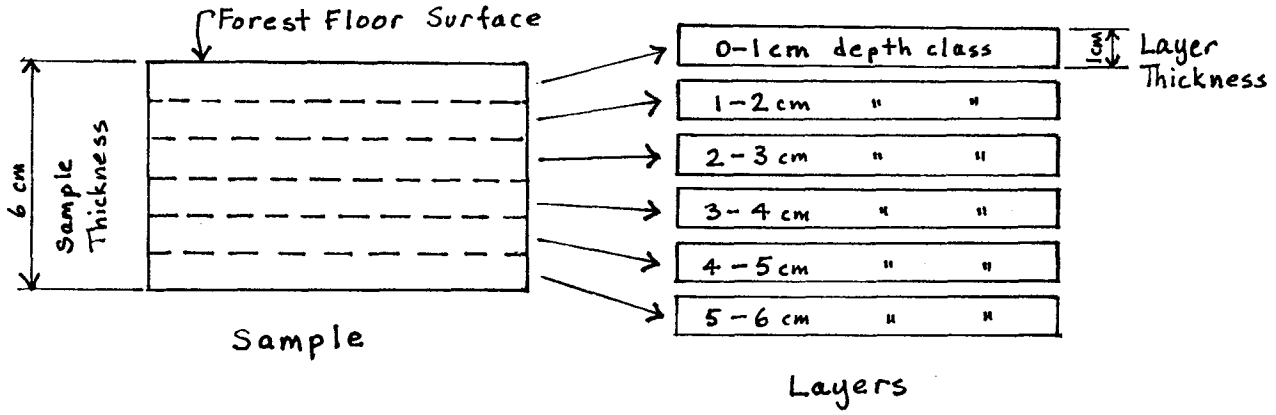

Figure 2.3 Example of the relationship between samples and layers, and between sample thickness, layer thickness and depth classes for the greenhouse samples.

in standard greenhouse trays (eight per tray). Containers were lined with remay to prevent loss of soil through the drainage holes, Sample splitting was completed on November 21, 1989. A few samples from each site crumbled during splitting and were therefore discarded. The total number of samples that were split for each site was 297 for the ESSF site and 301 for the ICH site.

From December 6 to 13, 1989 the greenhouse was heated with a kerosene heater but no temperatures were recorded. On December 15, 1989, samples were moved into a heated glass greenhouse at the Agriculture Canada Research Station on Saanich Peninsula, and thoroughly watered. Temperatures were maintained at 22^{o}C for 16 hours per day and 15^{o}C at night.

A few seeds germinated while the samples were still in the plastic-covered greenhouse. These were recorded on December 9, 1989. Data collection in the glass greenhouse started on December 20, 1989, and was carried out once per week until April 3, 1990, except for weeks 1, 3 and 4 when data were collected twice. Samples were allowed to dry out from April 4 to 10, then turned over and resoaked. Sampling resumed on April 17 and continued until April 24, 1990. The ESSF samples were moved outside onto benches, covered with remay to exclude seed rain and monitored from April 25 to May 29, 1990. Monitoring of the ICH samples ended on April 24 because very few seeds germinated after April 10.

Individual germinants were marked with coloured thread loops. A different colour was used each sampling date and loops were removed when germinants died. Thus, it was possible to determine which germinants were new each week, and to keep track

of them until they died, were identified, or were transplanted when further growth was necessary for identification.

Germinants were allowed to grow in the soil from which they originated until they were identifiable, and then were removed. Reference specimens for species that were not identified by April 3 were transplanted before the samples were allowed to dry out. The reference specimens were grown for several weeks but died before reaching maturity. Mature plants of some species were collected in 1990 from the study sites and identified, to indicate potential identities for some germinants.

2.2.2.2 Data analysis

Horizontal distribution of germinants among samples was examined by two methods. First, dispersion of germinants among samples was calculated as the percent presence of germinants of each taxon in the maximum number of samples the taxon could theoretically occupy. For taxa that had more germinants than there were samples (i.e. > 297 for the ESSF or 301 for the ICH sites, respectively), the assumption was made that the maximum number of samples that could be occupied was equal to the total number of samples. At maximum dispersion, these taxa would have > one germinant per sample. For taxa that had fewer germinants than there were samples, the maximum number of samples that could be occupied was defined as being equal to the number of germinants. At maximum dispersion, these taxa would have one germinant per sample. These calculations are therefore not influenced by the relative abundance of germinants in each taxon and thus allow

comparisons between taxa. The formula used for calculating dispersion was:

$$\frac{\text{number of samples occupied by a taxon X 100}}{\text{maximum number of samples the taxon could occupy}}$$

The lower this number was, the less dispersed (or more concentrated) the germinants were within the sampled area.

Second, the coefficient of variation of mean germinants per occupied sample was used as a measure of how evenly seeds were distributed among the samples in which they occurred. For example, two species could occupy the same number of samples but have very different distributions of seeds within those samples. The most uneven distribution would be a species with most of it's seeds in one sample and only one seed in each of the remaining samples. The other extreme would be a species with the same number of seeds in each sample occupied. The coefficient of variation allowed comparison among the taxa, which had different numbers of germinants occurring in different numbers of samples. The taxon with the highest coefficient of variation had the most uneven distribution.

The ranges of depths in the samples from which layers originated are referred to as depth classes. For example, all the layers that came from 2-3 cm in the samples belong to the 2-3 cm depth class, and so on. Samples varied considerably in thickness because only forest floor was collected, so the number of layers per depth class decreased with increasing depth. Therefore, two densities in germinants/m^2 were calculated for different purposes. These are referred to as total density and forest floor density.

Total density is the number of germinants in each depth

class divided by the total surface area sampled (2.97 m^2 for the ESSF site and 3.01 m^2 for the ICH site). This was used to examine vertical patterns of seed distribution. Forest floor density is the number of germinants divided by the actual area that was sampled in each depth class. This area decreased with increasing depth so forest floor density is the actual density of germinants in the forest floor only, for each depth class.

The data were graphed to assess whether there were discernable patterns with respect to depth. Large densities of germinants found in particular depth classes were examined to determine how uniformly germinants were distributed among the layers. This was important because a large clump of germinants in one sample could strongly skew the pattern of vertical distribution, resulting in a misinterpretation of the data.

2.2.3 **Field germination**

2.2.3.1 Data collection

Germination of seeds in the field was monitored in subplots and plots over the spring and summer of 1990. (See Section 2.2.1 for layout.) In the subplots, germination was recorded every two weeks from June 4 to August 22 on the ICH site and from June 10 to August 27 on the ESSF site. Individual germinants were marked with coloured thread loops, and identities and mortality were recorded.

On the ICH site all germinants in the 3 X 3 m plots were counted, marked and mapped at the same time as the subplots. The relatively high numbers of germinants in the ESSF plots and the density of existing vegetation in the unburned plots made mapping

and recording plot germinants impractical. A single count of all germinants surviving in the burned ESSF plots was made on the last recording date (Aug. 26, 1990). The timing of seed dispersal of species on or near the sites was observed in order to determine if any species of germinants originated from seed rain.

On October 13 1989, one Campbell Scientific CR10 datalogger per site was installed to record soil temperature over the next 10 months. On the ICH site relative humidity (RH) and air temperature were also recorded. On the ESSF site RH and air temperature data were obtained from another datalogger located approximately 100 m away. Each datalogger was located in an area close to both burned and unburned patches. Data loggers were placed in waterproof containers and temperatures were measured with thermocouples. After installation, thermocouple wires were covered with forest floor and slash (except over the ends), and the dataloggers were covered with plastic and logs to protect them from animal damage and provide insulation.

Thermocouples were placed at four locations, two in burned and two in unburned forest floor. On the ICH site thermocouples were placed at 1 and 2 cm from the surface at all four locations. At one burned and one unburned location, thermocouples were also placed at 4 cm depths. On the ESSF site, all four locations had thermocouples at 1, 2 and 4 cm from the surface. Data were recorded every five minutes, averaged and output once every 24 hours. Winter data collection ended June 5, 1990 for the ICH site and June 6, 1990 for the ESSF site.

During the summer of 1990, the dataloggers and thermocouples were left in place but data were averaged on an hourly basis.

Soil that is shaded has a lower temperature than soil exposed to the sun (Daubenmire 1968; Wells *et al.* 1979; Thompson and Grime 1983), providing a cooler germination environment for buried seeds. Therefore, starting June 18 (ICH site) and June 19 (ESSF site), and for the rest of the temperature recording period, one burned and one unburned location were shaded with slash. On the ICH site the locations with 1, 2, and 4 cm deep thermocouples were shaded. Summer temperature data were collected until August 24 on the ICH site and August 27 on the ESSF site.

2.2.3.2 Data analysis

Horizontal distribution of germinants was assessed by the same methods as those used in the greenhouse germination analysis (Section 2.2.2.2). Subplots were used in the analysis instead of samples. This analysis was carried out on ESSF data only, because there were no germinants in the ICH subplots.

Density of field germinants was calculated as the number of germinants divided by the area sampled in m^2 (0.75 m^2 for the subplots and 27 m^2 for the plots). Species composition and total density from the 0-1 cm depth class of the greenhouse samples were compared to those of the field subplots. The assumption was made that field germinants did not originate from > 1 cm deep in the forest floor. This provided the most conservative estimate of potential field germination, although it is possible that seeds did emerge from deeper in the profile. For the ICH site, total density in the plots was used because no germinants occurred in the unburned subplots.

Daily germination temperatures from field and greenhouse

were graphically compared. Air temperatures were used because soil temperature was not measured in the greenhouse. Hourly temperature cycles were also graphed for a few selected days using the greenhouse and ICH data only. Hourly air temperatures from the ESSF site were not available, but the soil data indicated patterns similar to those from the ICH site.

2.2.4 **Existing vegetation**

2.2.4.1 Data collection

Vegetation species presence and estimates of percent cover in the plots were recorded in 1989. These data provided information on possible sources of seed for some germinants, possible identity of germinants that could not be separated into species and divergence between the existing and former vegetation as represented by the seed bank.

2.2.4.2 Data analysis

Vegetation species composition and percent presence were tabulated with the taxa that germinated from the greenhouse samples and field plots and subplots. Percent presence was calculated as the number of plots, subplots or samples each species occurred in multiplied by 100 and divided by the total number of plots, subplots or samples. The inability to identify many of the germinants to species, however, made comparisons tentative.

2.3 Results and discussion

2.3.1 Greenhouse germination

2.3.1.1 Numbers and species

Unidentified germinants were grouped into dicotyledons and graminoids. The latter included Poaceae, Cyperaceae and Juncaceae germinants that could not be identified even to family. Poaceae probably included more than one species. *Vahlodea atropurpurea* and *Calamagrostis canadensis* were collected on the ESSF site and *Cinna latifolia* on the ICH site but it was not possible to determine whether the germinant grasses were these or other species. Both *Vaccinium membranaceum* and *V. ovalifolium* occurred on the sites but reference germinants were too small to distinguish between these species. An unknown Ericaceous species could have been *Menziesia ferruginea* on either site or *Rhododendron albiflorum* on the ESSF site. Two species of *Mitella* (*pentandra* and *breweri*) grew on the ESSF site but reference germinants died before the flowers essential for identification developed. The common sedge may have been either *Carex mertensii* or *C. spectabilis;* both were common in disturbed areas near the ESSF site.

Epilobium spp., other than *E. angustifolium*, may have dispersed some seed before samples were collected. However, no observations of seed dispersal at either site, were made during sampling. *Mitella* species were likely producing seed in an area adjacent to the ESSF site at the time samples were collected but no observations of plants with seeds were made in the sampling area. *Mitella* seeds, though very small, have no apparent adaptations for wind or animal dispersal and therefore were not

likely to have fallen on the sampling area. *Hieracium* spp. could have dispersed seeds onto the ICH site before sample collection. However, only one germinant (included in Asteraceae) was tentatively identified as *Hieracium*.

There were 2591 germinants (872/m^2) in total on the ESSF site, representing 13 taxa and unidentified dicotyledons (Table 2.1). The latter could have included several species, likely the same taxa that were already identified. More than half of the germinant taxa (excluding unidentified dicotyledons) were herbaceous plants, including four out of the five most abundant. Herbaceous taxa accounted for the vast majority of the germinants (94%, excluding unidentified dicotyledons) for this site. Ninety-six percent of the germinants belonged to the five most abundant taxa and unidentified dicotyledons. *Mitella* spp. accounted for 46% of the germinants, followed by *Luzula parviflora* 21%), unidentified dicotyledons (14%), *Carex mertensii* (8%), *Epilobium ciliatum* (4%), and *Vaccinium* spp. (4%) (Table 2.1). The standard error of total density among samples was relatively high for total germinants and for individual germinant taxa.

There were 689 germinants (229/m^2) in total on the ICH site, representing 16 taxa and unidentified dicotyledons (Table 2.2). Ninety-six percent of all germinants belonged to the five most common species and unidentified dicotyledons. Seven of the germinant taxa (44%) were shrubs but most of the germinants (75%) were trees. Herbaceous taxa accounted for only 6% of the germinants from this site. The most common species by far was *Thuja plicata* (72%), followed by *Vaccinium* sp. (9%), *Sambucus racemosa* (4%), *Epilobium ciliatum* (4%), unidentified dicotyledons

Table 2.1 The number of germinants by depth class and taxon, and total density of germinants ± the standard error of the mean by taxon, in the ESSF greenhouse samples. The proportions of germinants and layers per depth class are also given.

Taxon	Depth Class (cm) 0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	Total Density
Mitella spp.	363	312	279	171	35	20	3		1183	398 ± 51
Luzula parviflora	79	242	156	35	31	4			547	184 ± 31
Dicotyledons	133	79	61	52	14	12	1		352	119 ± 14
Carex spp.	1	6	27	39	73	68			214	72 ± 43
Epilobium ciliatum	58	36	6						100	34 ± 17
Vaccinium spp.	60	29	9		1				99	33 ± 6
Poaceae	29	7		1	8				45	15 ± 4
Ericaceae	9	5	10						24	8 ± 3
Sambucus racemosa	1	5	2	2	1				11	3 ± 1
Graminoids	1	5							6	2 ± 1
Picea sp.	5	1							6	2 ± 1
Galium sp.	2								2	<1
Ribes laxiflorum		1							1	<1
Valeriana sitchensis		1							1	<1
Total Germinants	741	729	550	300	163	104	4		2591	872 ± 82
Total Layers	297	283	191	83	33	11	2	1	901	
Percent Germinants	28.6	28.1	21.2	11.6	6.3	4.0	0.2			
Percent Layers	33.0	31.4	21.2	9.2	3.7	1.2	0.2	0.1		

Table 2.2 The number of germinants by depth class and taxon, and total density of germinants ± the standard error of the mean by taxon, in the ICH greenhouse samples. The proportions of germinants and layers per depth class are also given.

Taxon	Depth Class (cm) 0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	Total Density
Thuja plicata	477	17	1	1	1				497	165 ± 18
Vaccinium spp.	7	46	9	3					65	22 ± 11
Sambucus racemosa	1	16	6	4	2	1			30	10 ± 4
Epilobium ciliatum	10	8	5	2		2			27	9 ± 2
Dicotyledons	4	12	5	2		1			24	8 ± 2
Ericaceae	1	10	5						16	5 ± 2
Rubus idaeus	1	4	1						6	2 ± 1
Poaceae	2	2		1					5	2 ± 1
Asteraceae	2	2							4	1 ± 1
Anaphalis margaritacea	2	1							3	1 ± 1
Ribes laxiflorum	1	1	1						3	1 ± 1
Picea sp.	2								2	<1
Pinaceae	2								2	<1
Ribes sp.		1	1						2	<1
Graminoids			1						1	<1
Juncus ensifolius		1							1	<1
Rubus parviflorus				1					1	<1
Total Germinants	512	121	35	14	3	4			689	229 ± 21
Total Layers	301	299	259	125	35	12	3	1	1035	
Percent Germinants	74.3	17.6	5.1	2.0	0.4	0.6				
Percent Layers	29.1	28.9	25.0	12.1	3.4	1.2	0.3	0.1		

(4%) and Ericaceae (2%) (Table 2.2). The standard errors associated with total densities were relatively high for total germinants and for individual germinant taxa.

The proportion of unidentified germinants in other studies has varied considerably. Only one (Ingersoll and Wilson 1990), however, had more unknowns than the ESSF samples in this study. The authors did not discuss reasons for the relatively high numbers of unidentified germinants in their study. The proportion of unidentified germinants from the ICH samples was comparable to those reported by Archibold (1979), Kellman (1970), Strickler and Edgerton (1976) and Scheiner (1988). Other studies did not list unidentified germinants.

In this study germinants remained unidentified because they died before producing true leaves. None of the species had distinctive enough cotyledons to be able to assign identities with any confidence at that stage of development. The cause of death could not be determined in most cases but may have included faulty development, lack of nutrients in the sample, dehydration, insect damage, and fungal attack. Of these, the first two are more likely since samples were checked for moisture almost every day and damage by insects and fungi was not observed.

Germinants of genera such as *Mitella*, *Vaccinium* and *Epilobium*, that could not be separated into species, were likely species that were growing in the existing vegetation. *Mitella* spp. and *Vaccinium* spp. both grow in mature forests in the study area. *Epilobium* spp. were abundant in adjacent clearcuts and could have seeded into the site.

The number of taxa found on these sites was similar to other

comparable studies. Although taxa numbers from other studies ranged from 3 to 57, most had fewer than 20. Where both viable and non-viable seed content was determined, there were higher numbers of taxa. The high proportion of germinants that belonged to very few taxa in this study is typical of the distribution of seeds among taxa reported by several other researchers (Kellman 1970; Moore and Wein 1977; Granstrom 1982; Fyles 1989).

Most of the more abundant germinant taxa from both sites, or at least congenerics, have been found in temperate forest soil seed banks by other researchers. These include: *Sambucus racemosa* (Kellman 1970; Bormann and Likens 1979; Kramer and Johnson 1987; Granstrom 1988), other *Sambucus* species (Strickler and Edgerton 1976; Graber & Thompson 1978; Kramer and Johnson 1987; Morgan and Neuenschwander 1988a,b; Mladenhoff 1990), *Rubus idaeus* (Graber & Thompson 1978; Bormann and Likens 1979; Granstrom 1982, 1987, 1988; Fyles 1989), other *Rubus* species (Olmsted and Curtis 1947; Moore and Wein 1977; Morgan and Neuenschwander 1988a,b; Scheiner 1988), *Epilobium ciliatum* (formerly *E. watsonii*) (Kellman 1970, 1974; Strickler and Edgerton 1976; McGee 1988; Ingersoll and Wilson 1990), *Luzula parviflora* (Morin and Payette 1988), other *Luzula* species (Granstrom 1982, 1988, Kramer and Johnson 1987), *Carex mertensii* (Kellman 1970), other *Carex* species (Olmsted and Curtis 1947; Moore and Wein 1977; Whipple 1978; Archibold 1979; Kramer and Johnson 1987; Fyles 1989; Pratt, *et al.* 1984; Morin and Payette 1988; Mladenhoff 1990), non-viable *V. ovalifolium* seeds (Morin and Payette 1988), *Vaccinium* spp. other than *Vaccinium membranaceum* and *V. ovalifolium* (Kellman 1974; Granstrom 1982), *Mitella* spp. other than *M. pentranda* or *M.*

breweri (Strickler and Edgerton 1976; Kramer and Johnson 1987), and *Menziesia ferruginea* (Kellman 1974).

Thuja plicata was the only major taxon not found in other North American studies. The high number of *Thuja plicata* germinants from the ICH site may have resulted from the fact that, following logging, branches and foliage of this species were left on the ground where they deposited a large number of seeds.

The proportion of herbaceous to shrubby taxa among other studies shows no consistent pattern, similar to the results from this study. Most or all of the germinants from sites studied by Ingersoll and Wilson (1990), Kramer and Johnson (1987), Olmsted and Curtis (1947), Strickler and Edgerton (1976), and Whipple (1978) were herbaceous taxa. Shrub taxa were in the majority in studies by Kellman (1970) and Granstrom (1982).

Total density of greenhouse germinants in this study falls within the range found by comparable studies of mature forest soil seed banks. Densities of germinants in other studies range from approximately 100 germinants/m^2 to 1100 germinants/m^2. Comparison among studies is difficult, however, because of a wide variation in methodology. Densities from different studies are based on samples of different thicknesses and size, on samples of mineral soil as well as forest floor and on different sampling intensities.

The high variation in germinant density among samples in this study appears to be similar to or greater than that reported by a few previous studies. However, many researchers have either not included measures of variation or have obscured variation by

pooling samples. In addition, the measures of variation used are inconsistent from one study to another. Nevertheless, high sample to sample variation in germinant numbers has been recognized as a characteristic of soil seed banks, representing the uneven nature of seed distribution (Champness 1949; Major and Pyott 1966; Bigwood and Inouye 1988) and probably of burial forces (Garwood 1989).

Johnson (1975) proposed that seed bank densities decrease with increasing altitude and latitude. The high numbers of germinants in the ESSF site relative to the ICH site suggest that this is not the case. Overall site productivity related to moisture and nutrients may have resulted in a larger seed bank on the ESSF site, possibly through a higher rate of input and conditions more conducive to maintaining dormancy. This was suggested by (Fox 1983) as an explanation for the presence of, and variation among, arctic soil seed banks. Fyles (1989) has speculated that the vegetation history and species composition of sites are more likely causes of between-site variation in seed bank density than is latitude. Whipple (1978) and McGee (1988) both found that moister sites had more germinants than drier sites at subalpine and near sea-level elevations, respectively, while Morin and Payette (1988) observed a shift in species composition but no decrease in seed abundance with increasing altitude.

2.3.1.2 Horizontal distribution of germinants

The order of the five most abundant taxa from the ESSF site from least to most dispersed was: *Carex* spp. < *Epilobium ciliatum*

< *Luzula parviflora* < *Vaccinium* spp. < *Mitella* spp. (Table 2.3). *Carex* spp. germinants were much more concentrated than those of any other taxa. *Luzula parviflora* had a similar dispersion to *Epilobium ciliatum*, while *Vaccinium* spp. germinants. were almost as highly dispersed as those of *Mitella* spp.

For the ICH site, the order of the five most abundant germinant taxa from least to most dispersed was: *Vaccinium* spp. > Ericaceae > *Thuja plicata* > *Sambucus racemosa* > *Epilobium ciliatum* (Table 2.4). Ericaceae, *Thuja plicata* and *Sambucus racemosa* had similar dispersions, while *Epilobium ciliatum* was highly dispersed relative to the other taxa.

Most of the ICH taxa were more dispersed than the ESSF greenhouse germinants, although none of the more abundant taxa from either site occupied the maximum number of samples. In total, 18% of the ESSF samples and 32% of the ICH samples had no germinants at all. Germinant taxa from both sites showed no relationship between the degree of dispersion and number of germinants. For example, *Vaccinium* spp. (ESSF) was almost as dispersed as *Mitella* spp. but the latter was over 10 times as abundant. Similarly, *Thuja plicata*, from the ICH samples, had about the same dispersion as Ericaceae, but over 30 times the number of germinants.

Most of the more abundant germinant taxa from both sites had high coefficients of variation (C.V.), indicating relatively uneven, or clustered, distributions, among the samples in which each taxon occurred. Of the ESSF taxa, *Epilobium ciliatum* and *Carex* spp. had the highest C.V. *Mitella* spp. and *Luzula parviflora* had somewhat more even distributions that were

Table 2.3 Horizontal distribution of the five most abundant germinant taxa from ESSF greenhouse samples. Dispersion is the number of samples with germinants expressed as a percentage of the theoretical maximum number of samples. The coefficient of variation is a measure of how evenly germinants were distributed among the samples in which they occurred.

	Dispersion of Germinants			Evenness of Distribution[1]		
Taxon	Maximum Samples	Samples Occupied	Percent Presence	Mean	Standard Deviation	Coefficient of Variation
Carex spp.	214	16	7.5	13.4	30.1	224.9
Epilobium ciliatum	100	27	27.0	3.7	9.3	252.3
Luzula parviflora	297	90	30.3	6.1	8.2	134.4
Vaccinium spp.	99	47	47.5	2.1	1.9	89.8
Mitella spp.	297	146	49.2	8.1	11.0	135.9

[1] Based on the mean number of germinants per occupied sample.

Table 2.4 Horizontal distribution of the five most abundant germinant taxa from ICH greenhouse samples. Dispersion is the number of samples with germinants expressed as a percentage of the theoretical maximum number of samples. The coefficient of variation is a measure of how evenly germinants were distributed among the samples in which they occurred.

	Dispersion of Germinants			Evenness of Distribution[1]		
Taxon	Maximum Samples	Samples Occupied	Percent Presence	Mean	Standard Deviation	Coefficient of Variation
Vaccinium spp.	65	18	27.7	3.6	7.1	195.6
Ericaceae	16	8	50.0	2.0	1.6	80.2
Thuja plicata	301	158	52.5	3.1	3.6	116.0
Sambucus racemosa	30	17	56.7	1.8	1.9	108.9
Epilobium ciliatum	27	24	88.9	1.1	0.4	39.9

[1] Based on the mean number of germinants per occupied sample.

similar, while *Vaccinium* spp. had the most even distribution (Table 2.3). Among the ICH samples, *Vaccinium* spp. had the most uneven, and *Epilobium ciliatum* the most even distribution. *Thuja plicata*, *Sambucus racemosa* and Ericaceae fell between these extremes (Table 2.4). In general, the ICH taxa were more evenly distributed than the ESSF taxa.

Two germinant taxa common to samples from both sites, did not have the same dispersion or C.V. on both sites. *Vaccinium* spp. had almost the highest dispersion among ESSF samples but the lowest among ICH samples. Conversely, *Epilobium ciliatum* had the second lowest dispersion among ESSF samples but the highest among ICH samples. C.V. for *Vaccinium* spp. was lowest among ESSF samples and highest for ICH samples. *Epilobium ciliatum* had the highest C.V. among ESSF samples but the lowest among the ICH samples.

Seeds in forest soils probably have distributions that are always clumped to some degree because 1) source plants rarely have even distributions, 2) dispersal mechanisms tend to result in clusters of seeds, 3) burial forces are heterogeneous and 4) mortality both on and in the soil is likely to be spatially heterogeneous. Seed distribution of different species in the soil of a mature coastal forest in New Jersey ranged from nearly random to highly clustered (Matlack and Good 1990).

Seed clustering probably occurs at different scales depending on the disturbance history of the site, dispersal mechanism and microtopographical variation. Bigwood and Inouye (1988) concluded that seeds are likely clustered at all scales. The general relationship between dispersion and clustering in the

present study supports this. However, because the location of samples relative to each other in the field was not recorded and germinants were not mapped, conclusions can only be made about the degree of clustering, and not about the size and distribution of seed clusters at scales larger than the samples.

These data do show that each taxon had a range of distributions, from no seeds to single occurrences to large clusters in some cases. *Carex* spp., for example, had one germinant each in half the samples it occurred in, but 120 germinants in another sample. In contrast, the maximum number of seeds per sample for *Vaccinium* spp. (ESSF) was 10 and over 80% of the samples had three or fewer germinants of this taxon.

Major and Pyott (1966) have suggested that the small sample sizes typical of many seed bank studies result in unacceptably high variation among samples and therefore a poor estimate of seed numbers. Increasing sample size will reduce the standard error of the mean but will not decrease the variation in density among samples, given the inherently clustered distribution of seeds. The value of increasing sample size is in providing a better estimate of seed numbers by ensuring that the range of seed densities is sampled for each species. Results of this study and those of Bigwood and Inouye (1988) show that between-sample variation is probably a poor measure of the precision of such estimates. This study had a much larger number of samples per site than any other comparable project, but the S.E. of germinant density was still relatively high.

The differences in distributions of *Vaccinium* spp. and *Epilobium ciliatum* between the two sites may be the result of

sampling error associated with relatively rare, sporadically occurring large clusters interspersed with more evenly distributed, but still rare, small clusters. Alternatively, the different distributions may reflect differences between the sites such as seed input and dispersal.

The high number of samples, amounting to a relatively high total surface area, obtained from these sites, probably gave a reasonable estimate of the number of viable seeds for the more abundant taxa at least. However, because sampling was confined to a relatively small portion of each cutblock, species clustered at a larger scale may have been missed. For example, *Rubus parviflorus* germinants were observed on the ICH site within a few meters of the sampling area but only one germinant was recorded from the greenhouse samples.

2.3.1.3 Vertical distribution of germinants

Table 2.5 summarizes the proportion of samples of each thickness. The proportions by sample thickness of samples that had germinants, were similar to those of the total samples for both the ESSF and the ICH site. Samples from the ESSF site were approximately 3 cm thick on average, with the majority (84%) being 2 to 4 cm thick. Samples from the ICH site averaged 3.4 cm thick and most (88%) were from 2 to 4 cm thick.

Ninety percent of the ESSF greenhouse germinants came from the top 4 cm of forest floor. Almost the same proportion of germinants came from the 0-1 and 1-2 cm depth classes (29 and 20%, respectively), while the 2-3 cm and 3-4 cm depth classes accounted for 21% and 12% of the germinants, respectively. There

Table 2.5 Proportion of total greenhouse samples and samples that had germinants of each thickness, from the ESSF and ICH sites.

Sample Thickness (cm)	ESSF Samples		ICH Samples	
	% Total Samples	% Samples With Germinants	% Total Samples	% Samples With Germinants
1	4.7	4.1	0.7	0.5
2	31.0	28.5	13.3	13.7
3	36.4	34.6	44.5	41.7
4	16.8	18.3	29.9	31.9
5	7.4	8.9	7.6	8.3
6	3.0	3.7	3.0	2.9
7	0.3	0.4	0.7	0.5
8	0.3	0.4	0.3	0.5
% Total Samples With Germinants		82.8		67.8

were no germinants deeper than 7 cm (Table 2.1). A few *Mitella* spp. and unidentified dicotyledon germinants were found in the 6-7 cm depth class. *Luzula parviflora* and *Carex* spp. emerged from as deep as the 5-6 cm depth class, but *Epilobium ciliatum* and *Vaccinium* spp. were almost entirely confined to the top 3 cm of forest floor.

Of the five most abundant taxa of ESSF germinants, forest floor density of *Mitella* spp. and *Luzula parviflora* showed no pattern with respect to depth. *Carex* spp. appeared to increase sharply with depth, while *Epilobium ciliatum* and *Vaccinium* spp. showed a very slight decrease with depth (Figure 2.4). Forest floor density of all germinants summed increased with depth to 5-6 cm, then decreased sharply in the 6-7 cm depth class (Figure 2.5).

Total density of *Mitella* spp., *Epilobium ciliatum* and *Vaccinium* spp. decreased with depth (Figure 2.6). *Luzula parviflora* had the highest total density in the 1-2 cm layers, then decreased steadily with depth. Total density of *Carex* spp. germinants increased with depth to 4-5 cm, then decreased slightly. For all taxa combined, total density was similar for the top 2 cm, then decreased steadily with depth (Figure 2.5).

Seventy-four percent of the ICH greenhouse germinants came from the 0-1 cm depth class. *Thuja plicata* accounted for the majority of these (93%). The top 3 cm of forest floor contained 97% of all the germinants. All of the other more abundant taxa, except *Epilobium ciliatum*, had the highest proportion of germinants in the 1-2 cm depth class. There were no germinants in layers > 6 cm below the surface (Table 2.2). *Sambucus racemosa*

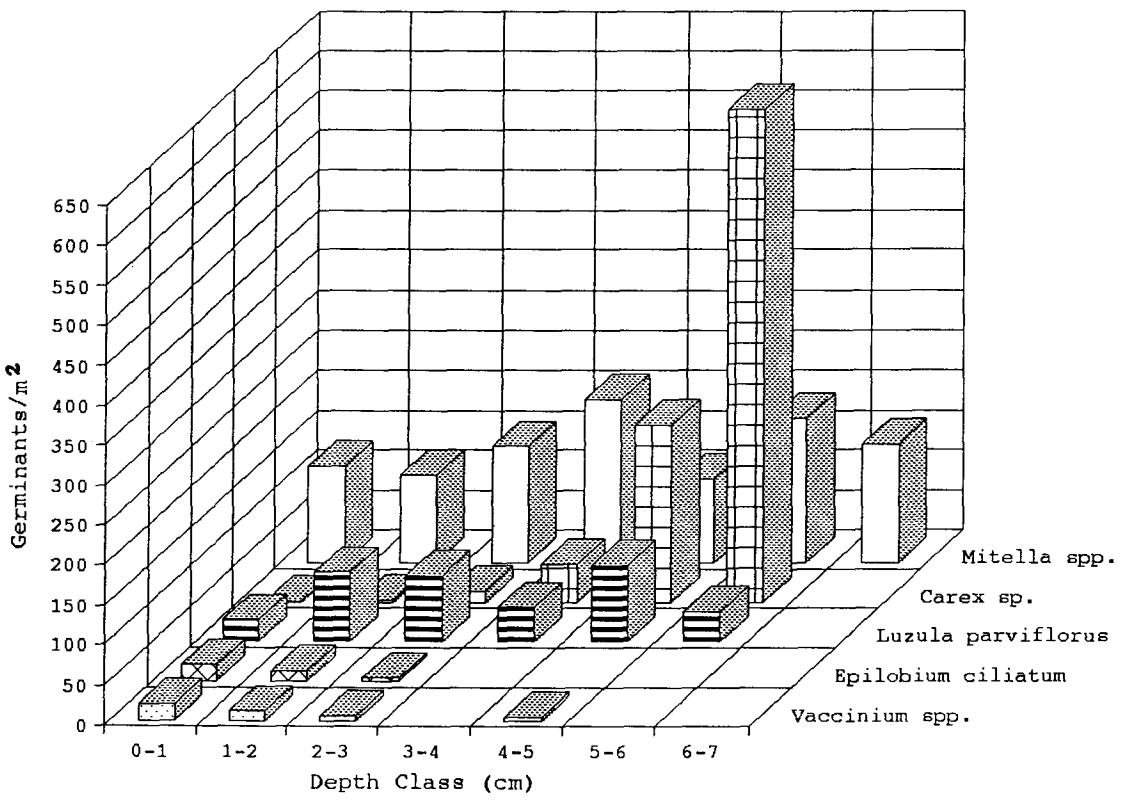

Figure 2.4 Forest floor germinant density as a function of depth for the 5 most abundant taxa in the ESSF greenhouse samples.

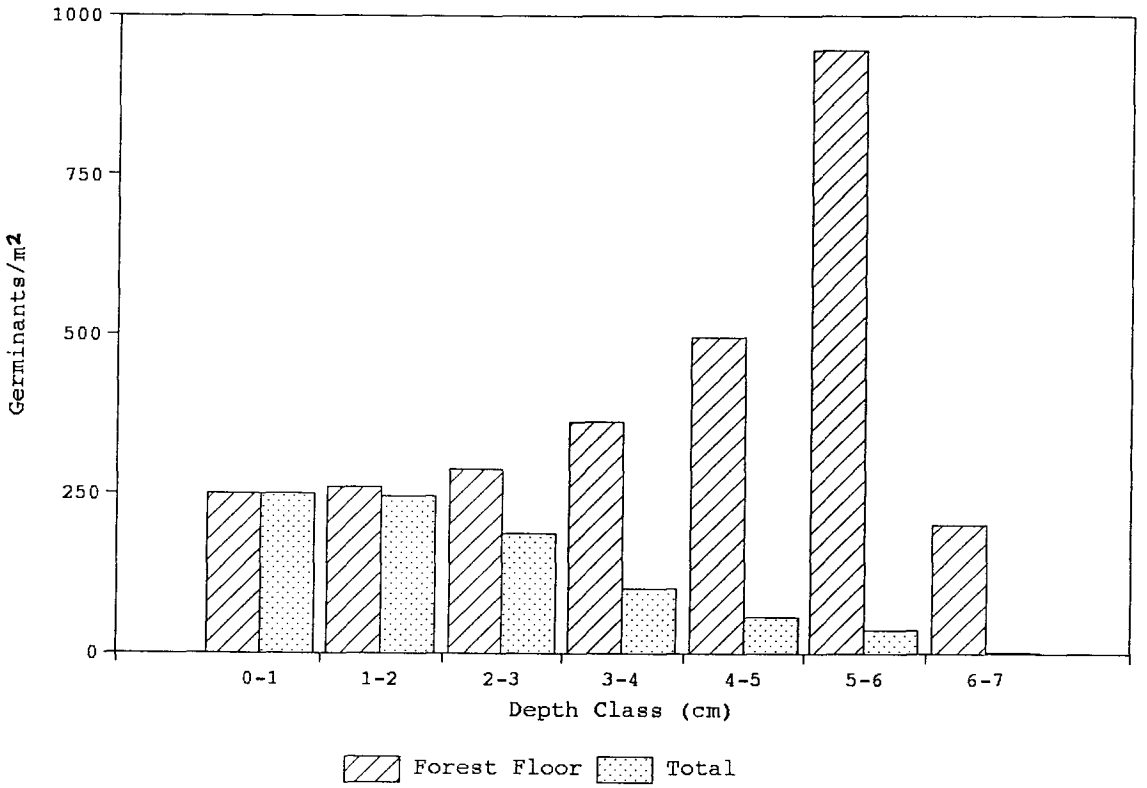

Figure 2.5 Forest floor and total density of all ESSF greenhouse germinants as a function of depth.

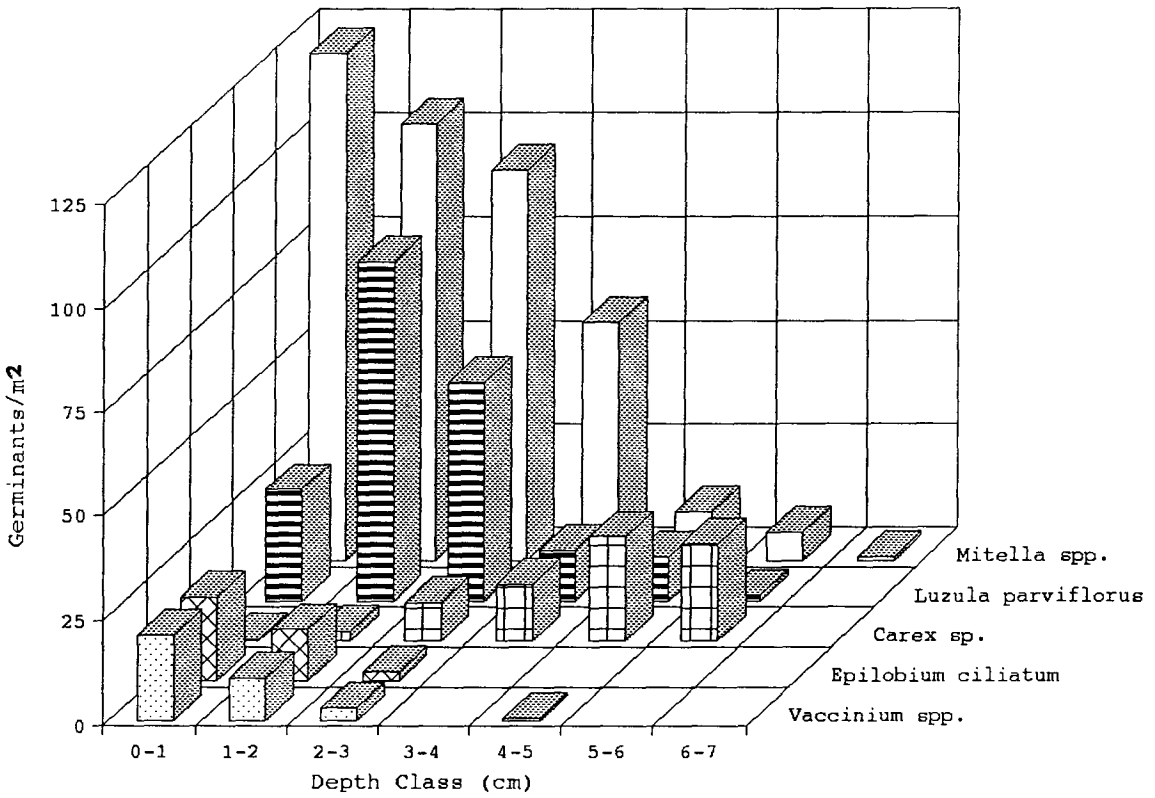

Figure 2.6 Total germinant density as a function of depth for the 5 most abundant taxa in the ESSF greenhouse samples.

density decreased sharply with depth (Figure 2.8). This pattern was similar to the distribution of *Thuja plicata* germinants because of the abundance of this species relative to other taxa (Figures 2.7, 2.9).

The patterns for *Carex* spp. and *Epilobium ciliatum* in the ESSF samples, and for *Vaccinium* spp. in the ICH samples, were strongly skewed by large clusters of germinants in very few samples. Eighty-eight% and 97% of the *Carex* spp. germinants from the 4-5 and 5-6 cm depth classes, respectively, came from two samples. Approximately 50% of the *Epilobium ciliatum* germinants in the 0-1 and 1-2 cm depth classes also came from a single sample. The relatively high forest floor density in the 1-2 cm ICH depth class for *Vaccinium* spp. was mainly the result of 30 germinants that emerged from one sample. These accounted for almost half of the total number of germinants for the taxon and 65% of the germinants in the 1-2 cm depth class. Therefore, the distributions of these three taxa were not consistent with respect to depth.

Several studies have shown a decrease in seeds with increasing depth (Kellman 1970; Strickler and Edgerton 1976; Moore and Wein 1977; Kramer and Johnson 1987; McGee 1988). In general, results from this study support these observations, although there is considerable variation in the patterns of individual taxa. Granstrom (1988) has pointed out, however, that was the only taxon to occur in all depth classes up to, and including, 5-6 cm. All *Vaccinium* spp. and most of the *Epilobium ciliatum* germinants occurred in the top 4 cm of forest floor. Ericaceae were not found deeper than the 2-3 cm depth class.

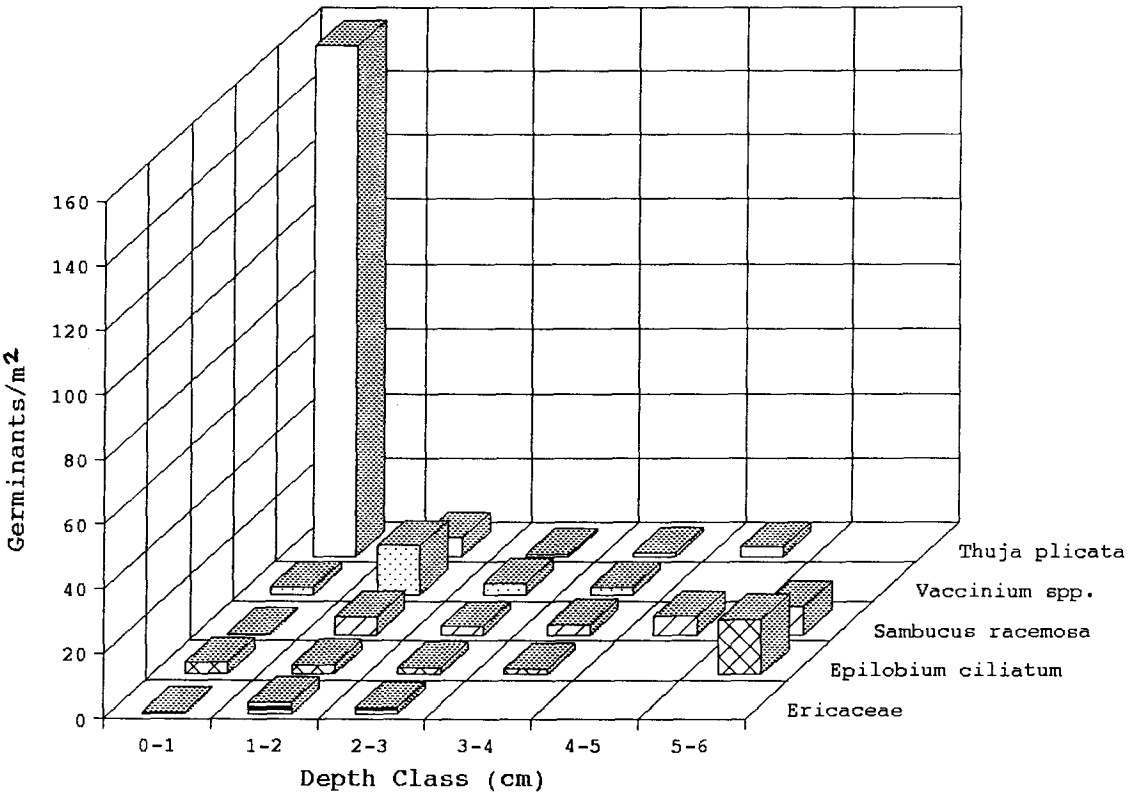

Figure 2.7 Forest floor germinant density as a function of depth for the 5 most abundant taxa in the ICH greenhouse samples.

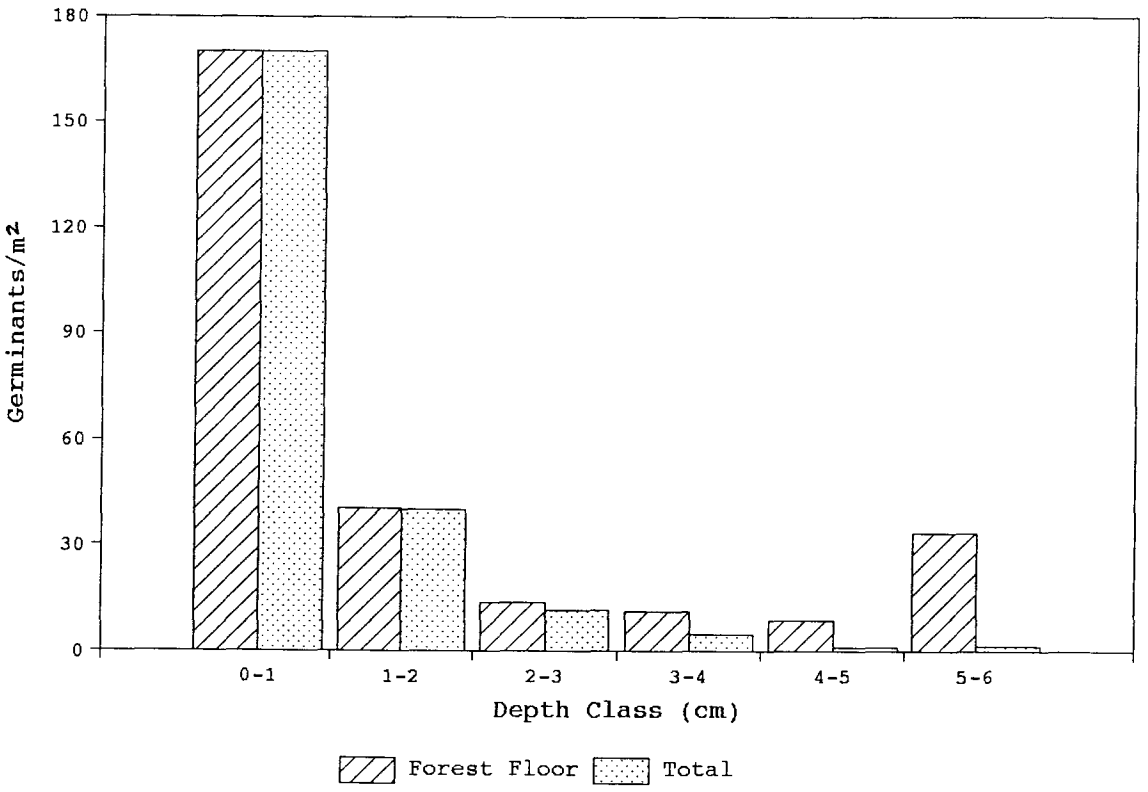

Figure 2.8 Forest floor and total density of all ICH greenhouse germinants as a function of depth.

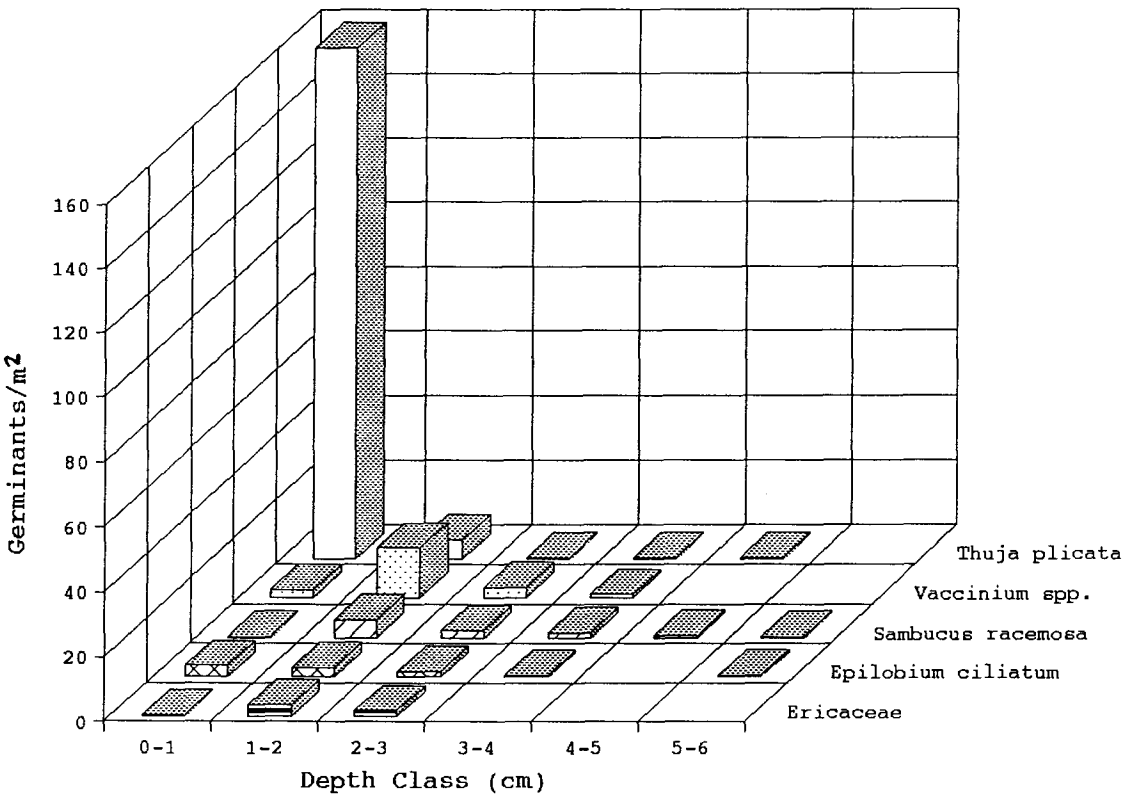

Figure 2.9 Total germinant density as a function of depth for the 5 most abundant taxa in the ICH greenhouse samples.

Forest floor density was generally low for all ICH taxa, other than *Thuja plicata*, at all depths, except for an increase in density of *Vaccinium* spp. germinants in the 1-2 cm depth class. (Figure 2.7). What appears to be a slight increase in forest floor density at 5-6 cm for *Epilobium ciliatum* and *Sambucus racemosa* was based on only three germinants in two samples and therefore cannot be considered a trend. When all germinants were summed, both forest floor density and total because this apparent trend is based on the means of all samples, the differences in patterns among individual samples are obscured. He also notes that adequate sample size has been addressed in relation to horizontal distribution, but not for variation in vertical distributions.

Results from both Granstrom (1988) and this study indicate that high variation exists in depth distributions among samples. Patterns that individual taxa exhibited in the present study were made up primarily of 1 or 2 cm thick clusters situated at different depths in different samples, rather than the same pattern of distribution within each sample. This means that differences in seed density with depth were the result of either differences in the mean number of seeds per cluster or differences in the number of clusters.

Another problem with previous determinations of depth distribution is a lack of resolution, either because the layers were relatively thick or because the sample was divided into only two or three layers. Other researchers have generally used 2 to 5 cm thick layers (Kellman 1970; Strickler and Edgerton 1976; Moore and Wein 1977; Granstom 1982; Kramer and Johnson 1987). Samples

divided into two layers (Kellman 1970; Kramer and Johnson 1987) can only indicate linear trends in distribution. For example, if the samples from the present study had been divided into 2 - 3 cm thick depth classes, *Luzula parviflora* would have shown a simple reduction in seeds with depth and the high densities in the 1-2 and 2-3 cm depth classes would have been missed.

The difference between the patterns of total and forest floor density can be explained by the fact that the proportion of layers per depth class decreased more than the proportion of germinants per depth class (Tables 2.1, 2.2). The increase in forest floor germinant density with depth for the ESSF site, suggests that seeds may be more concentrated in the deeper part of the profile. What is not known is whether there were seeds in the mineral layers corresponding in depth to the deeper forest floor layers, that would have moderated this distribution. If there were seeds in the mineral soil the pattern of distribution for total density would not decrease as much with depth or might not decrease at all.

The presence of *Mitella* spp. and *Sambucus racemosa* germinants throughout the ESSF and ICH profiles, respectively, could have been the result of continuous input over many years since both taxa grow in mature forests as well as earlier successional stages. *Luzula parviflora* and *Carex* spp. are more characteristic of disturbed habitats and are therefore more likely to have been deposited in an early successional stage, several decades ago or through small localized disturbances. *Epilobium ciliatum*, which was most abundant at 0-1 and 1-2 cm, may have been more recently deposited. Plants growing on

roadsides and older cutblocks in the vicinity of both sites could have been a source of wind-blown seed of this species in recent years. The *Thuja plicata* germinants in the 2-3, 3-4 and 4-5 cm depth classes probably originated from surface seeds that were accidentally dislodged during sample splitting.

Definite conclusions about the age of seeds in relation to location in the forest floor profile cannot be made without knowing the means of seed burial, the rate at which seeds move through the soil, if at all, and the specific longevity of seeds. Mature forest species could, however, have a shorter period of viability if they are able to contribute to the seed bank continuously. The fact that *Vaccinium* spp. germinants did not emerge from the deeper layers may mean that seeds of this taxon lose viability or are otherwise lost relatively quickly but are continually added to the seed bank.

2.3.2 **Field germination compared to greenhouse germination**

2.3.2.1 Numbers, species and distribution

Epilobium spp. germinants could have been either *Epilobium angustifolium* or *E. ciliatum*. Germinants that could not be identified even to family were all dicotyledons. Like the greenhouse germinants, (Section 2.3.1.1) Poaceae, *Vaccinium* spp. and *Mitella* spp. field germinants may have been the same species that grew on the sites. *Viola glabella* was common on both sites. On the ESSF site *Ribes lacustre* was the most common species of *Ribes* in the existing vegetation but *R. laxiflorum* was found as well.

Since seed rain was not excluded from the unburned areas, it

is possible that some germinants came from plants either on or near the plots. On the ESSF site Poaceae, *Epilobium* spp., *Valeriana sitchensis*, *Vaccinium* spp., *Mitella* spp. and *Viola glabella* could all have been dispersed onto the unburned plots during 1989. On the ICH site the unburned plots could have received seed rain from *Vaccinium* spp., *Epilobium* spp. and *Anaphalis margaritacea* in 1989. *Thuja plicata* may also have dispersed onto the plots from nearby trees or slash. *Epilobium angustifolium* almost certainly seeded in from nearby plants on both sites.

There were a total of 128 germinants ($171/m^2$) in the ESSF field subplots (Table 2.6). Of these, 39% were *Mitella* spp., 16% unidentified dicotyledons, 16% *Epilobium* spp., 11% Poaceae, and 5% *Vaccinium* spp. which together comprised 87% of the germinants.

The 0-1 cm depth class of the ESSF greenhouse samples had a higher density of germinants than the field subplots (Table 2.6). There were 11 taxa each (excluding unidentified dicotyledons) in both the greenhouse and field subplot germinants. Four of these taxa, and possibly five (*Epilobium* spp. may have been *E. ciliatum*), germinated in both.

In both the greenhouse samples and the field subplots, *Mitella* spp. had the highest density followed by unidentified dicotyledons. Of the remaining taxa that were the most abundant in the greenhouse germinants, *Epilobium* spp., Poaceae and *Vaccinium* spp. were also the next most abundant in the field subplots. *Luzula parviflora*, third most numerous taxon in the greenhouse was entirely absent from the field subplots.

Table 2.6 Number and total density (number/m^2) of germinants in the ESSF field subplots and 0-1 cm depth class of the greenhouse samples.

	Field Subplots		Greenhouse 0-1 cm	
Taxon	Number	Total Density	Number	Total Density
Mitella spp.	50	67	363	122
Dicotyledons	21	28	133	45
Poaceae	14	19	29	10
Vaccinium spp.	6	8	60	20
Picea sp.	1	1	5	2
Epilobium spp.	20	27		
Epilobium ciliatum			58	20
Pinaceae	4	5		
Ribes spp.	4	5		
Valeriana sitchensis	4	5		
Viola spp.	2	3		
Abies lasiocarpa	1	1		
Rubus spp.	1	1		
Luzula parviflora			79	27
Ericaceae			9	3
Galium sp.			2	<1
Carex spp.			1	<1
Graminoids			1	<1
Sambucus racemosa			1	<1
Total	128	171	741	250

Ericaceae, *Carex* spp. and *Sambucus racemosa* all had moderate numbers of germinants in deeper layers of the greenhouse samples but were not present in the field subplots. *Ribes* spp. occurred in the field subplots but not in the greenhouse germinants, although one *Ribes laxiflorum* germinant was found in the 1-2 cm depth class of a greenhouse sample.

No germinants were found in the ICH subplots. In the plots, however, there were a total of 22 germinants ($0.8/m^2$). One of the three plots did not have any germinants. Out of the 10 taxa in these plots only four had more than one germinant, and none had more than six. The four most abundant taxa were *Ribes* spp., *Epilobium* spp., *Sambucus racemosa* and *Thuja plicata* which together accounted for 73% of the germinants (Table 2.7).

The ICH greenhouse samples had a much higher number of germinants than did the field plots (Table 2.7). This result is especially striking because the field plots covered a 27 m^2 sampling area compared to only 3.01 m^2 for the greenhouse samples. Nine taxa (excluding unidentified dicotyledons) germinated in the field plots, compared to 12 from the greenhouse samples. Of these taxa, five were found among both greenhouse and field germinants. For all germinant taxa in both the field and greenhouse, germinant densities were higher in the greenhouse.

Epilobium angustifolium, *Epilobium* spp. and *Ribes* spp. germinants were found in the ICH field plots but not in the greenhouse samples. However, *Ribes laxiflorum* germinated from greenhouse samples and this may have been the species that occurred in the field. Similarly, the *Epilobium* germinants that were not identified to species in the field may have been *E.*

Table 2.7 Number and total density (number/m^2) of germinants in the ICH field plots and 0-1 cm depth class of the greenhouse samples.

	Field Plots		Greenhouse 0-1 cm	
Taxon	Number	Total Density	Number	Total Density
Thuja plicata	2	<1	477	159
Sambucus racemosa	4	<1	1	<1
Vaccinium spp.	1	<1	7	2
Dicotyledons	1	<1	4	1
Anaphalis margaritacea	1	<1	2	<1
Picea sp.	1	<1	2	<1
Rubus idaeus	1	<1	1	<1
Ribes spp.	6	<1		
Ribes laxiflorum			1	<1
Epilobium spp.	4	<1		
Epilobium angustifolium	1	<1		
Epilobium ciliatum			10	3
Asteraceae			2	<1
Pinaceae			2	<1
Poaceae			2	<1
Ericaceae			1	<1
Total	22	<1	512	170

ciliatum, which was the second most abundant taxon in the 0-1 cm depth class of the greenhouse samples. All other germinant taxa from the field plots were also found among greenhouse germinants. The four remaining taxa from the greenhouse samples that were not found in the field plots (excluding *Epilobium ciliatum* and *Ribes laxiflorum*) had only one or two germinants each.

In the ESSF field subplots, *Mitella* spp. had the lowest dispersion of the germinant taxa, followed by Poaceae, and *Epilobium* spp. (Table 2.8). The taxa ranked from most unevenly to most evenly distributed among the subplots where they were found were: *Epilobium* spp. > *Mitella* spp. > Poaceae (Table 2.8). The dispersion of *Mitella* spp. germinants was only slightly higher in the greenhouse samples than in the field (Tables 2.3 and 2.8). *Epilobium* sp. had much a lower dispersion in the greenhouse samples than in the field subplots. *Mitella* spp. and *Epilobium* spp. both had much more even distributions (*i.e.* lower coefficients of variation) in the field subplots than in the greenhouse samples.

Most of the genera, and some species, represented in the field germinants have been found in seed banks of other studies (see Section 2.3.1.1). In addition, *Ribes lacustre* (Kramer and Johnson 1987), other *Ribes* species (Olmsted and Curtis 1947; Strickler and Edgerton 1976; Kramer and Johnson 1987), *Viola glabella* (Kramer and Johnson 1987), other *Viola* species (Olmsted and Curtis 1947; Strickler and Edgerton 1976; Graber and Thompson 1978; Granstrom 1988; Morin and Payette 1988; Ingersoll and Wilson 1990; Mladenoff 1990) and *Anaphalis margaritacea* (Kellman 1970, Pratt *et al.* 1984), have also been recorded. There were no

Table 2.8 Horizontal distribution of the three most abundant germinant taxa from ESSF field subplots. Dispersion is the number of subplots with germinants expressed as a percentage of the theoretical maximum number of subplots. The coefficient of variation is a measure of how evenly germinants were distributed among the subplots in which they occurred.

	Dispersion of Germinants			Evenness of Distribution[1]		
Taxon	Maximum Subplots	Subplots Occupied	Percent Presence	Mean	Standard Deviation	Coefficient of Variation
Mitella spp.	50	26	52.0	1.9	1.1	56.8
Poaceae	14	11	78.6	1.3	0.5	36.7
Epilobium sp.	20	16	80.0	1.3	0.8	62.0

[1] Based on the mean number of germinants per occupied subplot.

references to *Valeriana sitchensis*. Granstrom (1987) has shown that *Epilobium angustifolium* does not maintain dormancy for more than a year so germinants of this species in the field probably came from recently arrived seed.

There are no comparable studies of field germination from forest floor exposed to light *in situ*. Several researchers have suggested that the results of greenhouse germination may be biased because of an inability of this method to provide the conditions that all species need to break dormancy and germinate (reviewed by Roberts 1981). Results from this study indicate that germination from greenhouse samples provided a good representation of the major taxa that germinated under field conditions, although this does not mean that all seeds and species in the soil germinated. In a few cases, likely congenerics were identified in the greenhouse germination. The absence in the field of some of the minor greenhouse germinant taxa may have been the result of the low probability of sampling these species, either because of extremely patchy distributions or very low numbers of germinants. Alternatively, some of these taxa may not have been part of the seed bank at all but originated from recent seed rain instead.

The greenhouse germinant taxa that were not found in the field may, in the case of the ESSF, be the result of a smaller sample area in the field. The absence of *Luzula parviflora* and *Carex* spp. germinants in the field may have been because the seeds of this taxon were not as abundant in the surface of the forest floor.

The fact that the total density was higher in just the top

cm of the greenhouse samples suggests that the greenhouse may have provided better germination conditions than the field. Studies by McGee (1988) and Ingersoll and Wilson (1990) have shown that samples germinated in a greenhouse environment had significantly more germinants than samples that were kept outside.

In the present study, higher greenhouse germinant densities may have been the result of a longer period of germination: 135 (ICH) to 166 (ESSF) days compared to 80 days for field germination. However, when greenhouse germinants that had emerged after 80 days were tallied, there was a lower total density for the ESSF greenhouse samples (127 germinants/m^2) than for the field germinants. ESSF greenhouse germinants did not reach the same density as the field germinants until 124 days after the start of monitoring. In addition, most of the field germinants (87%) had emerged by only 56 days from the start of monitoring. Despite the lower density of greenhouse germinants after 80 days, all but one taxon present at 166 days were already present after 80 days.

In contrast, the total density of ICH greenhouse germinants was higher than the final field density only 14 days after the start of monitoring, even when *Thuja plicata* was excluded. All but one minor greenhouse germinant taxa was present by the 80th day of monitoring. Thus, for the ICH site, greenhouse conditions appear to have been more favourable to germination than field conditions. Field germinants may have been rare because seeds were unable to germinate in the thick moss cover of the unburned area, which may have insulated seeds from higher temperatures or

wider temperature fluctuations, or because there was insufficient moisture.

As with the greenhouse samples, the horizontal distribution of germinants in the ESSF field subplots was clustered at both scales that were examined. The generally higher dispersion and more even distributions of the field germinants may have been due to the smaller number of samples, the fact that distribution of greenhouse germinants was based on germination from the whole forest floor profile, of some other factor.

2.3.2.2 Field and greenhouse germination compared to field vegetation

Four taxa found in the original vegetation also occurred as germinants in both the ESSF field subplots and greenhouse samples (Table 2.9). *Mitella* spp., which had the highest presence and abundance of the germinant taxa, was very common in the vegetation. *Valeriana sitchensis*, *Vaccinium* spp. and Poaceae also occurred in the field vegetation and as germinants.

Luzula parviflora was the only species common to both germinants and field vegetation that had a higher percent presence in the greenhouse samples than in the field plots. This taxon was not found among field germinants. Two taxa (*Viola* spp. and *Abies lasiocarpa*) were found as field germinants and vegetation but were not among greenhouse germinants. In addition, the *Ribes* spp. germinants found in the field subplots may have been *R. lacustre* which was present in the existing vegetation. *Epilobium* spp. and *Epilobium ciliatum*, which were relatively common and abundant as germinants, were absent from the vegetation. *Carex* spp. was an important greenhouse germinant taxa

Table 2.9 Percent presence of the ESSF taxa in field vegetation, and in greenhouse and field germinants.

	Percent Presence		
	Field Vegetation	Greenhouse Germinants	Field Subplot Germinants
Taxa in Common			
Mitella breweri	91.7		
Mitella spp.		49.2	34.7
Vaccinium membranaceum	91.7		
Vaccinium ovalifolium	91.7		
Vaccinium spp.		15.8	6.7
Valeriana sitchensis	100.0	0.3	4.0
Menziesia ferruginea	83.3		
Rhododendron albiflorum	66.7		
Ericaceae		4.0	
Poaceae	33.3	8.4	14.7
Luzula parviflora	8.3	30.3	
Viola spp.	91.7		2.7
Abies lasiocarpa	8.3		1.3
Ribes lacustre	41.7		
Ribes spp.			5.3
Unique Taxa			
Gymnocarpium dryopteris	100.0		
Streptopus roseus	100.0		
Tiarella unifoliata	100.0		
Veratrum viride	91.7		
Athyrium filix-femina	58.3		
Arnica sp.	50.0		
Dryopteris assimilis	33.3		
Rubus pedatus	16.7		
Clintonia uniflora	8.3		
Moneses uniflora	8.3		
Pyrola minor	8.3		
Picea sp.	+	1.3	1.3
Epilobium ciliatum		9.1	
Carex spp.		5.4	
Sambucus racemosa		3.0	
Graminoid		1.3	
Galium sp.		0.7	
Ribes laxiflorum		0.3	
Epilobium spp.			21.3
Pinaceae	+		2.7
Dicotyledons		37.7	18.7
n	12	297	75
Total Area (m^2)	108	2.97	0.75

+ = Taxa present as trees before logging.

that was also missing from the field vegetation.

The field vegetation had many more taxa than either greenhouse or field germinants. Percent presence of field vegetation was generally much higher than either field or greenhouse germinants. Several species, including *Streptopus roseus*, *Tiarella unifoliata*, and *Veratrum viride*, had high presence (> 90%) in the ESSF field vegetation but were entirely absent from the identified germinants.

Vaccinium spp. and *Thuja plicata* occurred in the existing or pre-harvest ICH vegetation and as field and greenhouse germinants (Table 2.10). The unknown ericaceous species was the only other germinant taxon that may have occurred in the existing vegetation, possibly as *Menziesia ferruginea*. This taxon was only found as germinants in the greenhouse samples, not in the field plots.

Clintonia uniflora, *Cornus canadensis*, *Rubus pedatus*, *Streptopus roseus* and *Tiarella unifoliata* all had > 90% presence in the existing vegetation but did not occur as germinants. The germinant taxa *Epilobium* (*E.* spp. in the field and *E. ciliatum* in the greenhouse), *Sambucus racemosa* and *Rubus idaeus* were not found in the existing vegetation but were found as germinants in both the greenhouse and the field. The number of taxa present in the vegetation was slightly higher than for the greenhouse germinants but much higher than for the field germinants.

For both sites, the generally lower percent presence of taxa as germinants than as existing vegetation species probably reflects the difference in sample unit size (0.01 m^2 vs 3 m^2 for germinants and existing vegetation, respectively). *Vaccinium* spp.

Table 2.10 Percent presence of the ICH taxa in field vegetation, and in greenhouse and field germinants.

	Percent Presence		
	Field Vegetation	Greenhouse Germinants	Field Plot Germinants
Taxa in Common			
Thuja plicata	+	52.5	33.3
Vaccinium membranaceum	90.9		
Vaccinium ovalifolium	90.9		
Vaccinium spp.		6.0	33.3
Menziesia ferruginea	36.4		
Ericaceae		2.7	
Unique Taxa			
Clintonia uniflora	100.0		
Cornus canadensis	100.0		
Gymnocarpium dryopteris	100.0		
Rubus pedatus	100.0		
Streptopus roseus	100.0		
Tiarella unifoliata	90.9		
Lycopodium annotinum	72.7		
Orthilia secunda	54.5		
Goodyera oblongifolia	27.3		
Viola spp.	27.3		
Dryopteris assimilis	18.2		
Linnaea borealis	18.2		
Streptopus amplexifolius	18.2		
Oplopanax horridus	9.1		
Sorbus scopulina	9.1		
Veratrum viride	9.1		
Sambucus racemosa		5.6	66.7
Rubus idaeus		2.0	33.3
Anaphalis margaritacea		1.0	33.3
Picea sp.	+	0.7	33.3
Ribes sp.		0.7	33.3
Epilobium ciliatum		8.0	
Asteraceae		1.3	
Poaceae		1.3	
Ribes laxiflorum		1.0	
Graminoids		0.3	
Juncus ensifolius		0.3	
Pinaceae	+	0.3	
Rubus parviflorus		0.3	
Epilobium angustifolium			33.3
Epilobium sp.			66.7
Dicotyledons		6.3	33.3
n	12	301	3
Total Area (m^2)	108	3.01	27

+ = Taxa present as trees before logging.

and possibly Ericaceae were common to vegetation and germinants in both the ESSF and ICH sites indicating some consistency of response in these species.

The relatively low similarity between the species composition of vegetation and germinants on the ICH site has been found in other studies of forest soil seed banks (Roberts 1981; Archibold 1989). The ESSF site may have had more taxa in common because the characteristics of the ecosystem favoured species that bank seeds. For example, there may have been a more open canopy or more frequent small disturbances resulting in small gaps that allowed enough light into the understory for forest species to produce seeds. Other studies (Matlack and Good 1990; Mladenoff 1990) have indicated that such gaps may provide for replenishment of the seed bank through local reproduction of some forests species that can only produce seeds in gaps.

Of the six taxa possibly common to ESSF greenhouse germinants and vegetation, *Mitella* spp. and *Vaccinium* spp. are probably most important. These two taxa account for almost 50% of the total greenhouse germinants from the ESSF site. Therefore, even though species composition was not very similar, a substantial proportion of the seed bank originated from species that grow in forests, rather than species characteristic only of early successional stages.

2.3.2.4 Temperatures during germination monitoring in the greenhouse and field study sites

Field and greenhouse daily and hourly temperature patterns were different even though actual temperature ranges overlapped.

Throughout the germination periods, temperatures ranged from 6.1 to 31.5°C for the greenhouse, 0.8 to 31.2°C on the ICH site and -1.3 to 29.9°C on the ESSF site. Mean temperatures for the recording period were lower in the field than in the greenhouse (20.5, 12.0 and 15.1°C for the greenhouse, ESSF site and ICH site respectively).

The greenhouse temperature stayed mainly between 15 and 25°C throughout the recording period. In the field, temperatures generally increased over the summer at both the sites (Figure 2.10). Field temperatures showed greater fluctuation than greenhouse temperatures, especially the maxima. The mean of the daily ranges of temperatures for the germination monitoring periods was highest in the ICH field site (13.7°C), but similar in the ESSF field site and the greenhouse (10.1 and 9.0°C, respectively).

Field temperatures showed a pattern of change over a day with a rise toward afternoon followed by a drop at night. Variation in greenhouse temperatures occurred on an hourly basis and the main difference at night was that there was less fluctuation in temperature (Figure 2.11).

The differences in temperature fluctuation patterns could help account for the differences between greenhouse and field germination results in either species composition or numbers of germinants. Without specific tests, however, little can be concluded about the influence of the temperature regimes on germination since other factors, such as moisture, disturbance, monitoring frequency and shading, varied as well.

ICH greenhouse samples probably received more moisture than

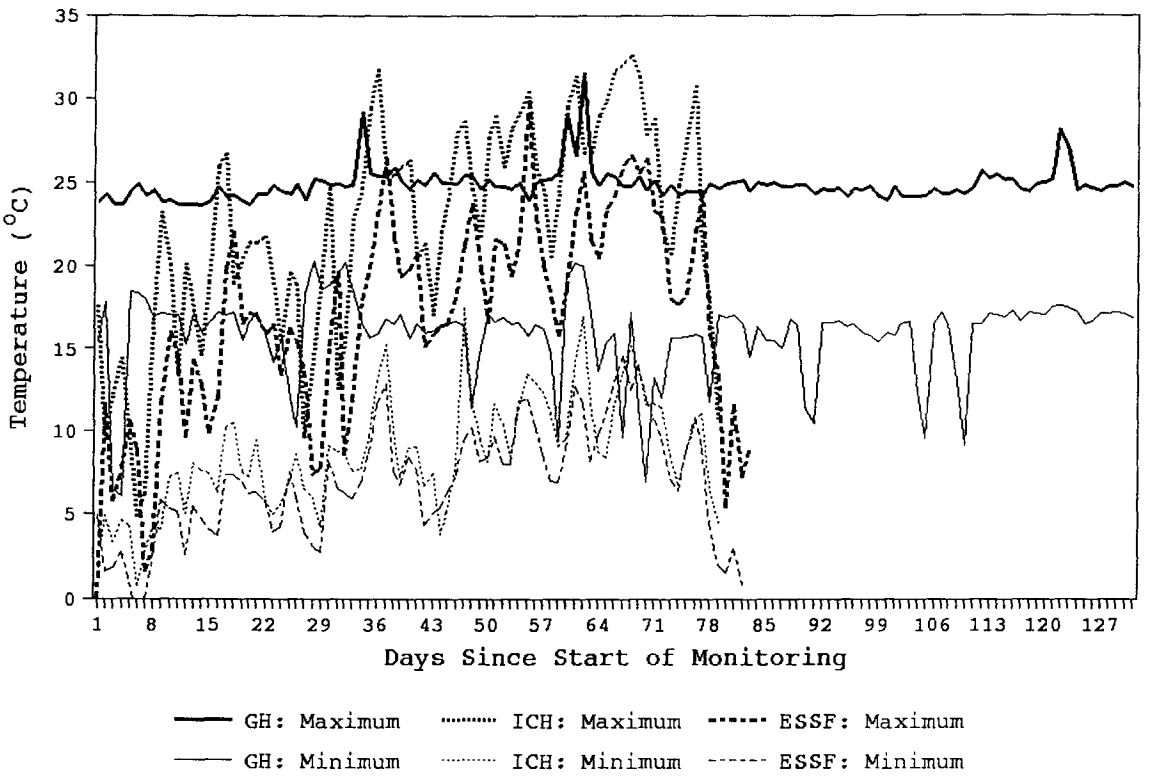

Figure 2.10 Daily maximum and minimum air temperatures recorded during the germination monitoring periods on the ESSF and ICH field sites, and in the greenhouse.

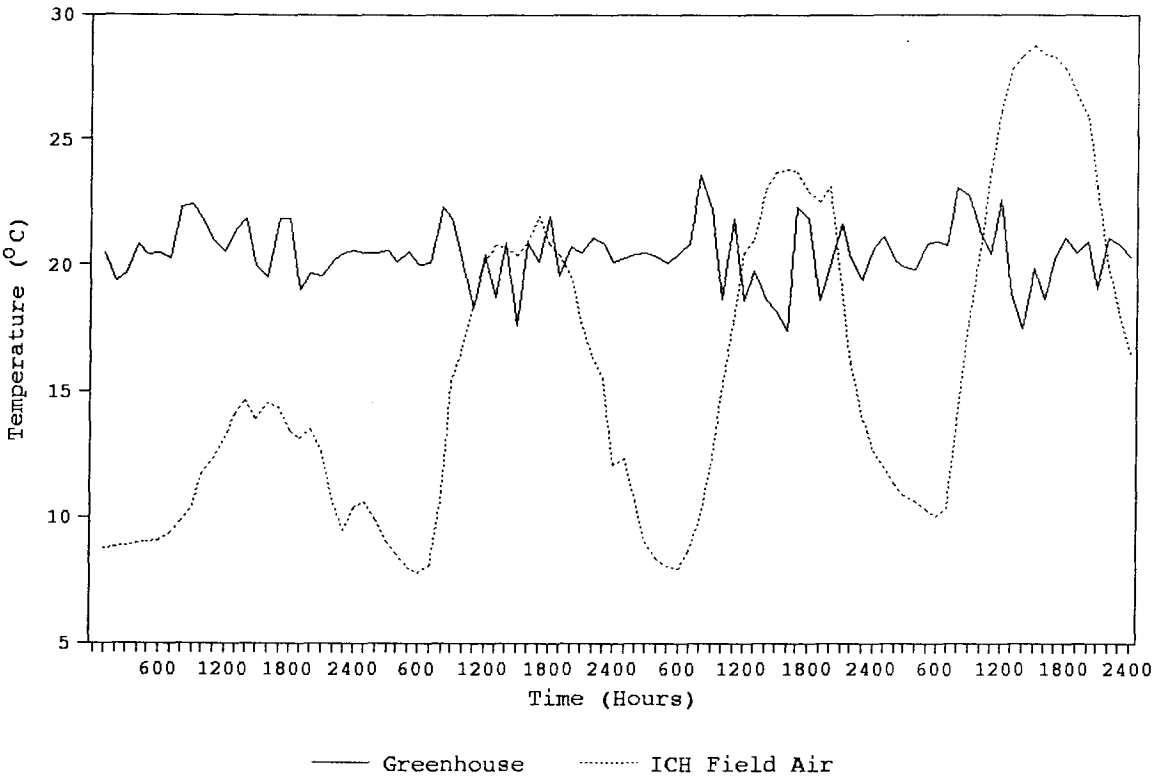

Figure 2.11 Typical pattern of hourly average air temperatures over a 4 day period in the greenhouse (Jan. 25-28, 1990) and at the ICH field study site (July 7-10, 1990).

did the ICH field plots, which could have explained greater germination in the greenhouse. Lower soil moisture may also have allowed soil temperature to rise higher, possibly to lethal levels for seeds. Shading in the field, especially in the ESSF site, could have inhibited germination by lowering soil temperatures. The fact that greenhouse samples were monitored more frequently and were split into layers, thus exposing more of the profile to air and light, may also have contributed to the higher germinant densities observed in the greenhouse.

2.4 Conclusions

The density of germinants, number of taxa and variation in germinant numbers among samples, appeared to be within the ranges encompassed by other comparable to other greenhouse germination studies of northern temperate forest soils. Almost all of the major germinant taxa, or related species, from both greenhouse and field have been found in other comparable studies.

The greenhouse germination appeared to provide a reasonably good estimate of the numbers and species composition of the more abundant seed bank taxa, although some relatively rare taxa that germinated in the field were not present in the greenhouse samples. The greenhouse germination overestimated the number of field germinants and included some taxa not found in the field. Therefore, while greenhouse germination may provide information on the total seed bank, it will not always predict what will germinate in the field.

This study indicates that there is a significant number of buried seeds in the forest floor of moist ESSF sites, and that

many of these will germinate after logging, even if the forest floor is not further disturbed. The taxa that germinated in the field tended to be those whose seeds were more abundant in the 0-1 cm depth class of the greenhouse samples.

In contrast, a much smaller seed bank was present in the greenhouse samples from the ICH site and very few seeds germinated in the field. Therefore, germination from seed banks does not appear to be an important means of regeneration of any species on mesic ICH sites. This result also shows that site productivity, along with vegetation history and stand structure, is probably more important than altitude in determining the extent of the buried seed population.

Horizontal distribution of the most abundant greenhouse germinant taxa was clustered at both scales examined. Germinants were concentrated into smaller areas than the maximum possible and showed relatively uneven distributions within the samples in which they occurred. The relative abundance of germinants per taxon was not related to the horizontal distribution of germinants. The degree of dispersion and clustering varied greatly among the germinant taxa.

Despite a very large number of samples compared to other studies, variation in germinant density among samples was high. This indicates that, while increasing sample size may increase the precision with which seed numbers are estimated, between-sample variation is not a good measure of that precision.

Vertical distribution of germinants was highly varied both among and within taxa. Although overall results showed increasing, decreasing and centre-peak distributions with

increasing depth, closer examination of individual samples revealed two important facts. First, the observed patterns were made up of individual relatively thin (1 to 2 cm) clusters of seeds located at different depths in the profile, rather than a consistent pattern found in each sample. Second, the distributions of some taxa were highly skewed by one or two very large clusters of germinants in one or two samples. The implication of these findings for sampling is that relatively large numbers of samples are required not only to assess seed numbers and species but also to describe the three-dimensional distribution of buried seeds. In addition, samples must be divided into many relatively thin layers to provided good resolution of the patterns of vertical distribution of germinants.

Some germinant taxa that grow in disturbed areas had more seeds deeper in the forest floor profile, suggesting that input may have decreased over time. Another early successional taxon - *Epilobium* spp. - was located closer to the surface of the profile indicating more recent origin through wind-blown seed dispersal. However, nothing is known about the burial mechanisms at work on seeds in these sites and therefore it cannot be concluded that there is a relationship between vertical distribution and seed age.

Taxa that grow in mature forests and those characteristic of early successional disturbed habitats were both present among seed bank germinants from both sites. In the ESSF site a large proportion of the germinants were of mature-forest taxa. Continuous seed input over many years may have been the means

through which these taxa maintained seed banks. The clustered nature of both the vertical and horizontal distribution of germinants, however, suggests that periodic, small disturbances created gaps in the forest which stimulated seed production. If forest plantations are managed for a dense canopy, species that rely on these disturbances to maintain seed reserves, may be lost or severely reduced.

Differences in the temperature regime between greenhouse and field environments may help to explain differences in germination between these locations. However, these differences may have resulted from a number of other factors, such as reduced daylength in the greenhouse, lack of moisture in the ICH field site, and disturbance in the greenhouse in the form of sample splitting. The latter may have stimulated higher seed germination. Alternatively, the higher density of greenhouse germinants may be due to the longer period and greater frequency of germination monitoring, particularly for the ICH samples.

Given the wide variation in temperature conditions under which seeds germinated in both the greenhouse and the field, the requirements for germination do not appear to be very narrow for any taxon. While there may have been taxa that did not germinate because a narrow set of requirements was not met, this is not very probable since such a strategy is unlikely to evolve in a temperature environment that is highly varied.

CHAPTER 3 THE EFFECTS OF FIRE ON THE SEED BANK

3.1 Introduction

Dormancy and germination in seeds are known to be influenced by temperature, light, moisture, and chemistry (Mayer and Poljakoff-Mayber 1982; Bewley and Black 1985). Of these, the changes in the soil temperature environment, both during and after burning, are likely to have a profound effect on buried seeds. Burning elevates soil temperatures during the fire, and usually results in higher temperatures and more extreme diurnal fluctuations in temperature in the growing seasons after the burn (Wells *et al.* 1979; Feller 1982). Fire severity, which determines a) soil temperature during (magnitude and duration), and after (magnitude and fluctuation) the fire, and b) quantity of surface organic matter removed, and the characteristics and vertical distribution of buried seeds, will determine how seeds are affected by fire.

Fire is an important source of disturbance in both unlogged forests and after logging in the south central interior of B.C. During the 1988/89 to 1990/91 fiscal years, wild fires burned 3048 ha of forest, while slashburning was carried out on 31,748 ha (36% of the area harvested during this period) in the Kamloops Forest Region (B.C. Ministry of Forests 1989, 1990, 1991). Although such burning has been practiced for many years to manage vegetation, reduce fire hazard and increase planter access, relatively few studies have attempted to determine whether vegetation management objectives are being met. In interior and northern B.C. no studies have specifically addressed the response

of seed banks to fire. It is particularly important to determine how plants respond to fire in areas where fire is not a frequent event, if the natural diversity of these communities is to be maintained. However, the nature of post-burn conditions in the soil has not been assessed in relation to the germination requirements of seeds.

During forest fires and slashburns seed mortality may result from direct combustion of seeds along with the forest floor, or from lethal temperatures being reached in the forest floor profile. More moderate temperatures deeper in the profile may stimulate germination or have no effect on seeds. Germination could also be affected by the alteration in the post-fire temperature environment. The magnitude and duration of elevated temperatures can determine whether or not seed mortality occurs (Stone and Juhren 1951; Went *et al.* 1952; Floyd 1966). High temperatures for very short periods may do less damage, for example, than prolonged exposure to more moderate temperatures.

There is little information on the patterns of forest floor heating during actual fires. Data are relatively difficult to collect with a sufficiently large sample size to adequately characterize the considerable variation that occurs during most fires. Forest floor consumption is another measure of fire severity that is simple to collect and might provide an indication of heating during burns if a relationship could be established between depth of burn and heating in the remaining forest floor.

The specific objectives of this component of the study were to:

1) quantify the effects of slashburning on germination from seed banks of burned forest soils in the ESSF and ICH zones in south central British Columbia;

2) quantify temperatures in the forest floor during slashburning;

3) determine if there is a relationship between forest floor temperature and depth of burn during a slashburn; and

4) quantify the effects of shading and burning on post-burn soil temperatures and on germination of buried seeds.

3.2 **Methods**

3.2.1 **Study areas**

Intensive studies were carried out on one ESSFwc2 and one ICHwk1 site. These sites were both operationally slashburned in the fall of 1989. The layout of plots and subplots on these sites is described in detail in Chapter 2, Section 2.2.1.

In 1990, six additional ICH and seven ESSF sites in the Clearwater Forest District were surveyed for germinants (See Chapter 2 Figure 2.1 for site locations). These sites had all been logged during the winter of 1988/89 and operationally slashburned in the fall of 1989 and are hereafter referred to as 'extensive sites'. Four of the ICH sites were located in the Thompson Moist Warm variant (ICHmw3), the remaining two were in the ICHwk1. All ESSF sites were in the ESSFwc2 variant (Table 3.1).

Identification of these sites was tentative because sampling

Table 3.1 Identification of the extensive field study sites according to the Biogeoclimatic Ecosystem Classification system.

Site Number	Location	Zone and Variant	Site Series	Moisture Regime
1	S. Foam Ck.	ESSFwc2	07 to 08	Subhygric to Hygric
2	Chalet Rd.	ESSFwc2	01	Mesic
3	Barriere Mt.	ESSFwc2	01	Mesic
4	Wallace Ck.	ESSFwc2	(01) to 07	(Mesic) to Subhygric
5	Wallace Ck.	ESSFwc2	07	Subhygric
6	Fowler Ck.	ESSFwc2	07	Subhygric
7	Camp 6 Ck.	ESSFwc2	01	Mesic
1	Berry Ck.	ICHmw3	07 to 08	Subhygric to Hygric
2	Berry Ck.	ICHmw3	05	Submesic
3	Finn Ck.	ICHmw3	04 & 08	Submesic and Hygric
4	Otter Ck.	ICHmw3	04	Submesic
1	S. Foam Ck.	ICHwk1	01 to 05	Mesic to Subhygric
2	S. Foam Ck.	ICHwk1	06	Subhygric

was carried out after slashburning and therefore many key plant species were missing. Nevertheless, a range of site series from each variant appeared to be represented (Lloyd *et al.* 1990). Some of the ESSF sites were identified before burning for another research project.

The ESSFwc2 sites (Table 3.1) included Azalea - Feathermoss (05), Azalea - Oak fern (01), Devil's club - Lady fern (07), and Horsetail - Sphagnum (08) site series. ICHwk1 site series were Oak fern (01), Devil's club - Lady fern (05) and Devil's club - Horsetail (06) (Table 3.1). ICHmw3 site series included Soopolallie - Twinflower (04), Falsebox (05), Devil's club - Oak fern (07) and Skunk cabbage (08) (Table 3.1). Some sites included more than one site series because of varied small-scale topography.

3.2.2 **Field germination**

3.2.2.1 Data collection

Methods for collecting field germination data for both burned and unburned areas of the intensive sites are outlined in Chapter 2, Section 2.2.3.1.

On each extensive site nine 0.5 X 0.5 m plots were located 5 m apart along a transect. The total area sampled per site was 2.25 m^2, equal to the area of the burned subplots on each intensive site. Transects were subjectively located in areas that were representative of the cutblock in terms of species composition and abundance. Sampling was carried out from July 21 to 23, 1990. All germinants inside each plot were counted and identified if possible.

3.2.2.2 Data analysis

Density was calculated for germinants of all taxa in the burned subplots and plots of the intensive sites and plots on the extensive sites. Germinant density was calculated on a per m^2 basis. Species composition of germinants in the extensive sites was examined to assess the ecological distribution of seed bank taxa found in the intensive sites.

3.2.3 **Effects of fire**

3.2.3.1 Data collection

During the 1989 burns, soil temperatures were recorded under four subplots each in three of the burned plots. Temperature data were collected with a Campbell Scientific CR10 data logger and 36 channel multiplexer. At each location thermocouples were buried at 1, 2 and 4 cm below the forest floor surface. Eleven of the 1 cm thermocouples were coated Chromel-Alumel wire, connected directly to the data logger. The remaining thermocouples were coated Copper-Constantine wire connected to the multiplexer which was, in turn, connected to the data logger.

The data logger and multiplexer were enclosed in metal boxes and wrapped in plastic garbage bags to exclude moisture and soil. They were buried in a hole under approximately 30 cm of mineral soil. Thermocouple wires were buried in trenches under approximately 10 cm of mineral soil. Temperatures were recorded every 10 seconds, averaged, and output once per minute. In both cases the datalogger was excavated and stopped as soon as possible the day after the burn.

The ESSF site was burned on September 14, 1989 and the ICH

site was burned on October 9, 1989. The codes and indices of the Canadian Fire Weather Index System (Canadian Forestry Service 1984) at the time of burning for the ESSF site were: FFMC=86, DMC=11, DC=47, ISI=7, BUI=14 and FWI=9. When the ICH site was burned, the codes and indices were: FFMC=82, DMC=29, DC=165, ISI=2, BUI=41 and FWI=5.

As a result of technical problems, only temperatures less than 100^{o}C were recorded during the 1989 ICH burn and data from the 1989 ESSF burn were unusable. Therefore, on September 20, 1990, temperatures were recorded during operational slashburning of another ESSF cutblock near the intensive ESSF site. For this burn, two Campbell Scientific CR10 data loggers and Chromel-Alumel thermocouple wire were used to record forest floor temperature at four locations. Thermocouples were installed at 1, 2, 3, 4, and 6 cm below the surface at all four locations. At three locations an additional thermocouple was placed at 10 cm and at one of these locations there was also a thermocouple at the forest floor surface. All other procedures were similar to the 1989 burns.

Depth of burn was measured using pins made of 2.4 mm steel welding rod bent to a right angle with the measurement arm 12 cm long. The pins were placed at each of the 25 subplots per plot in the area to be burned (see Figure 2.2 for layout). Pins were installed (Figure 3.1) and litter depth recorded in July and August of 1989. A single measurement of litter depth was made just outside each subplot, to avoid disturbing the seed bank. Forest floor consumption (depth of burn) was recorded within two days after the sites were burned. Depth of burn was measured at

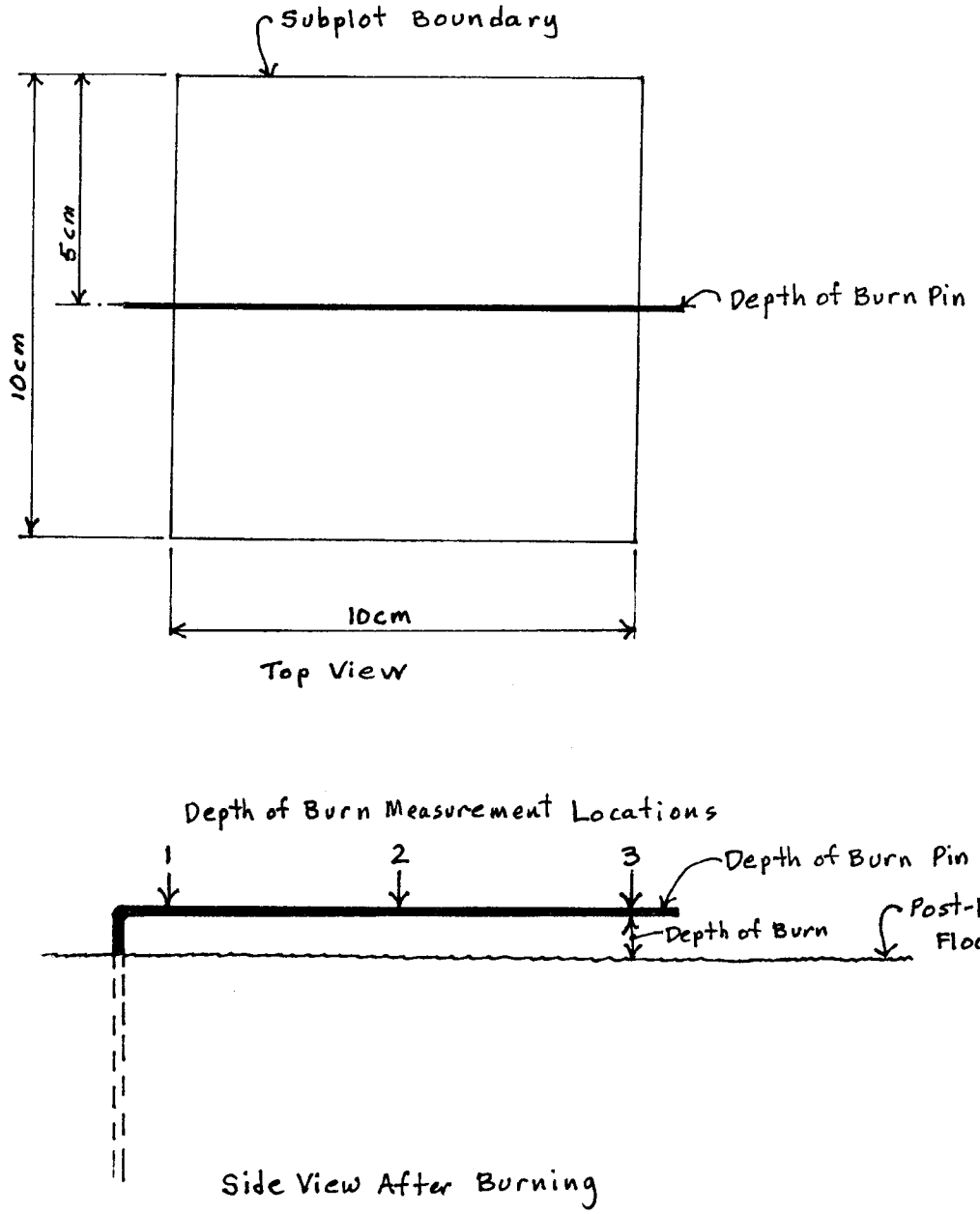

Figure 3.1 Placement of depth of burn pins over the subplots and measurement of forest floor consumption on the intensive study sites.

the middle and 1 cm from each end of the arm of the pins (Figure 3.1).

On the 1990 burn three depth of burn pins were installed with the arms parallel and five cm apart over each group of thermocouples (Figure 3.2). Three measurements were taken along each pin for a total of nine per thermocouple location, the day after the burn.

3.2.3.2 Data analysis

The number of minutes that temperatures were > 60, 70 and 100°C was determined for each location and depth in both the 1989 ICH burn and the 1990 ESSF burn. Number of minutes > 80°C was also determined for the 1990 ESSF burn. The duration of temperatures over 60, 70 80 and 100°C was correlated with the mean depth of burn of the subplots (SAS 1988). Correlation analysis was also used to determine if there was a relationship between mean depth of burn and maximum temperature reached during the 1990 ESSF burn for the 1, 2 and 4 cm depths.

The mean depth of burn was calculated for each subplot and plot. Thirteen subplots were excluded from the ESSF analysis because the pin had been disturbed before sampling and depth of burn could not be determined. However, all 225 subplots were used for germination analyses that did not involve depth of burn. Four extra subplots were installed on the ICH site to accommodate available lengths of thermocouple wire, for a total of 229 burned subplots, all of which had reliable measurements.

An estimate of seeds consumed along with the forest floor was calculated as a partial determination of seed mortality. The

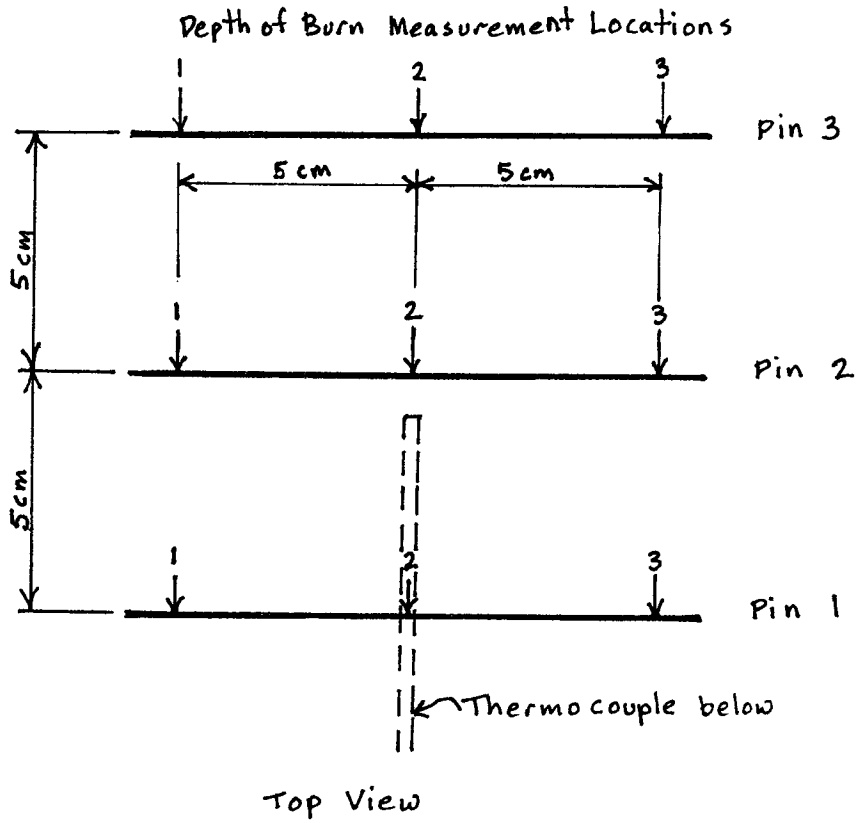

Figure 3.2 Placement of depth of burn pins over the thermocouples on the ESSF site burned in 1990.

potential number of seeds in each subplot was based on the mean number of greenhouse germinants per 1 cm thick layer in each depth class. Seed consumption was calculated as the percentage of the depth class consumed, for each subplot. Since depth of burn was measured to the nearest 0.1 cm, consumption was calculated in 10% increments. For example, a depth of burn of 0.3 cm was translated into consumption of 30% of the estimated seeds in the 0-1 cm depth class.

Estimations of seed consumption and remaining seeds are based on the assumptions that a) the greenhouse germination represented seed numbers and distribution in the field, and b) that the vertical distribution of seeds was uniform within depth classes. Because both distribution and numbers of germinants were found to be highly variable in the greenhouse samples, however, these estimates probably contain some error.

The relationship between the total number of germinants and average depth of burn in the burned subplots and plots was examined using correlation analysis. The data on germinants and depth of burn both deviated severely from normal distributions, thus violating one of the assumptions of correlation analysis. Since neither log nor square-root transformations resulted in normally distributed data, the non-parametric rank correlation procedure of Spearman (Zar 1974) was employed (SAS 1988). Numbers of germinants of individual taxa in the plots were also correlated to depth of burn, but there were too few germinants in the subplots to be analysed by species.

To further examine the effect of fire on germination, an estimate was made of the number of seeds remaining in the post-

burn 0-1 cm layer of each subplot. This estimate was then compared to the number of germinants per subplot by depth of burn. Statistical analysis of the difference between the numbers of germinants and remaining seeds was not appropriate, however, because the latter was estimated.

As with seed consumption, estimates of remaining seeds were based on the number of germinants/layer in each greenhouse depth class. In subplots where the post-burn 0-1 cm of forest floor overlapped two pre-burn depth classes, the proportion of each depth class occupied was used to calculate remaining seeds. For example, 0-1 cm in subplots with a 1.4 cm depth of burn was equivalent to the pre-burn 1.4 to 2.4 cm depths, and therefore 60% of the estimated remaining seeds came from the pre-burn 1-2 cm depth class and 40% from the pre-burn 2-3 cm depth class.

3.2.4 **Post-burn soil temperatures and shading in the intensive study areas**

3.2.4.1 Data collection

See Chapter 2, Section 2.2.3.1 for details of field temperature data collection. Percent shading was also estimated for each subplot, to determine whether germination was affected. The four combinations of 'treatment' conditions for both temperature and germination were: shaded/burned, shaded/unburned, unshaded/burned and unshaded/unburned.

3.2.4.2 Data analysis

Since there was no replication of the soil temperature measurements on the sites, statistical analysis of the

differences between treatment means was not appropriate. Mean temperatures were based on repeated measurements at each treatment location and were therefore not independent of each other. The first 13 days were excluded from calculation of the mean temperatures because the thermocouples had not yet been shaded. Due to malfunctions in the temperature recording systems some data were unusable. Thirty-nine days of data were excluded from the shaded/unburned location of the ESSF site and 13 days of data were excluded from the shaded/burned location of the ICH site.

The effects of burning and shade on field germination in the ESSF subplots were examined with 'goodness of fit' analysis to test the null hypothesis that the ratio of germinants per treatment was the same as the ratio of subplots per treatment. The frequencies of subplots per treatment were considered the expected ratios for this analysis. Germinants in all burned versus all unburned subplots were tested first. Germinants in shaded versus unshaded subplots within the burned and unburned treatments were then tested. There were too few germinants in the ICH subplots to be analysed statistically.

In all three tests, the number of degrees of freedom was 1. Therefore the Yates correction for continuity was employed to reduce the possibility of rejecting a true null hypothesis (Type I error) due to an inflated, calculated chi-square statistic (Zar 1974). In this procedure, 0.5 is subtracted from the absolute value of each observed frequency - expected frequency value used to calculated the chi-square statistic.

3.3 **Results and discussion**

3.3.1 **Field germination after burning**

3.3.1.1 Germination on the burned intensive sites in comparison to the unburned seed bank and pre-burn vegetation

It is possible that some species were dispersed onto the sites after the fire, thus contaminating the seed bank of the burned plots. Nearby plants of *Epilobium angustifolium* were observed to have seeds which could have been blown onto both sites after the fire. However, seeds of fruit-bearing species such as *Ribes* spp., *Vaccinium* spp., and *Sambucus racemosa*, that could have been carried onto the burned plots by animals or birds, had little or no fruit left by the time the site was burned.

A total of 49 germinants ($22/m^2$) in 36 (16%) of the 225 burned ESSF subplots was recorded during the first post-burn growing season (Table 3.2). On the last sampling date (Aug. 26, 1990), 715 ($9/m^2$) germinants were recorded in the burned plots. The total density was much higher in the unburned subplots than in the burned subplots and plots.

There were eight germinant taxa plus unidentified dicotyledons in the burned ESSF subplots. The most abundant were unidentified dicotyledons and *Epilobium* spp. (27% each), *Epilobium angustifolium* (14%), and *Ribes* spp. (10%). These accounted for 78% of the germinants (Table 3.2). In addition to most of the taxa found in the burned subplots, *Epilobium ciliatum*, *Carex* spp., *Ribes laxiflorum*, *Cirsium* sp. and *Hieracium* sp. germinants were found in the burned plots on the last sampling date.

Table 3.2 Number and density (number/m^2) of germinants in the burned and unburned field plots and subplots and in the greenhouse samples from the ESSF intensive site.

	Burned Seed Bank Germinants				Unburned Seed Bank Germinants			
	Field Subplots		Field Plots		Field Subplots		Greenhouse Samples	
Taxon	Number	Density	Number	Density	Number	Density	Number	Density
Poaceae	1	<1	5	<1	14	19	45	15
Epilobium angustifolium	7	3	359	4				
Epilobium sp.	13	6			20	27		
Epilobium ciliatum			33	<1			100	34
Ribes lacustre	3	1	89	1				
Ribes spp.	5	2	1	<1	4	5		
Ribes laxiflorum			2	<1			1	<1
Viola spp.	3	1	53	<1	2	3		
Luzula parviflora	1	<1	8	<1			547	184
Sambucus racemosa	3	1	136	2			11	4
Carex spp.			24	<1			214	72
Mitella spp.					50	67	1183	398
Vaccinium sp.					6	8	99	33
Picea sp.					1	1	6	2
Valeriana sitchensis					4	5	1	<1
Cirsium spp.			1	<1				
Hieracium spp.			1	<1				
Abies lasiocarpa					1	1		
Pinaceae					4	5		
Rubus sp.					1	1		
Ericaceae							24	8
Graminoid							6	2
Galium sp.							2	<1
Dicotyledons	13	6	3	<1	21	28	352	119
Total	49	22	715	9	128	171	2591	872
n	225		9		75		297	
Area (m^2)	2.25		81		0.75		2.97	

Poaceae was the only germinant taxon to be recorded in all burned and unburned ESSF seed banks assessments. *Luzula parviflora*, *Sambucus racemosa* and *Viola* spp. also germinated from both burned and unburned forest floor but not from all unburned seed banks. *Carex* spp. germinated only in the burned plots and greenhouse samples. The highly clustered distribution of this taxon may account for it's absence from the burned subplots. *Viola* spp. germinants were missing from the greenhouse samples, which may indicate that this taxon originated from recent seed rain, rather than from the seed bank. Both *Luzula parviflora* and *Sambucus racemosa* were missing from the unburned subplots, which could have been a function of the much smaller sampling area involved compared to the burned seed bank or greenhouse samples.

Epilobium spp. germinants were found in all four ESSF seed bank assessments but were not identified to species in the unburned field subplots. *E. angustifolium* was the most abundant species in the burned plots but was absent from the greenhouse samples, where only *E. ciliatum* was recorded. Similarly, *Ribes* spp. germinants were found in both burned and unburned seed banks but were not identified to species in the unburned subplots. These germinants could have been either *R. lacustre* which was only found in the burned seed bank, or *R. laxiflorum* which was identified in both the burned plots and greenhouse samples. Because of these overlaps, it was not possible to determine whether or not *Epilobium angustifolium* and *Ribes lacustre* germinated only from burned forest floor.

Cirsium sp. and *Hieracium* sp. were identified only from the burned ESSF plots. Only one germinant of each was recorded,

however, and both have wind-dispersed seeds that could have originated from off-site sources during the germination monitoring period. Two of the most abundant unburned seed bank taxa, *Mitella* spp. and *Vaccinium* spp., were missing from the burned plots and subplots. *Valeriana sitchensis* and *Picea* sp. were also found only in the unburned subplots and greenhouse samples. In addition, Ericaceae germinants were only found in the greenhouse samples.

Epilobium angustifolium was the most abundant taxon in five of the ESSF plots. *Sambucus racemosa* had the most germinants in two plots, and *Ribes lacustre* and *Viola* spp. were most abundant in one plot each.

During the first growing season 14 ($6/m^2$) germinants emerged in 13 (6%) of the 229 burned ICH subplots. Half these germinants were unidentified dicotyledons. Of the remainder, three were *Ribes laxiflorum*, two were *Ribes lacustre*, and one each were *Rubus idaeus* and *Ribes* spp. (Table 3.3). In the burned ICH plots 504 germinants ($6/m^2$) were recorded. *Sambucus racemosa* was the most abundant (35%) followed by *Rubus idaeus* (16%), unidentified dicotyledons (14%), *Ribes laxiflorum* (10%), *Paxistima myrsinites* (8%) and *Ribes* spp. (7%). These accounted for 90% of the germinants in the burned plots (Table 3.3). Burned plots and subplots both had much higher germinant densities than did the unburned plots.

Rubus idaeus was the only germinant species found in all four ICH seed bank assessments. *Sambucus racemosa*, *Anaphalis margaritacea* and Poaceae germinants occurred in both burned and unburned seed banks, although all three were missing from the

Table 3.3 Number and density (number/m^2) of germinants in the burned and unburned field plots and subplots and in the greenhouse samples from the ICH intensive site.

	Burned Seed Bank Germinants				Unburned Seed Bank Germinants			
	Field Subplots		Field Plots		Field Plots		Greenhouse Samples	
Taxon	Number	Density	Number	Density	Number	Density	Number	Density
Rubus idaeus	1	<1	81	1	1	<1	6	2
Ribes laxiflorum	3	1	50	<1			3	1
Ribes spp.	1	<1	35	<1	6	<1	2	<1
Ribes lacustre	2	<1	15	<1				
Epilobium angustifolium			9	<1	1	<1		
Epilobium spp.			1	<1	4	<1		
Epilobium ciliatum							27	9
Sambucus racemosa			178	2	4	<1	30	10
Anaphalis margaritacea			8	<1	1	<1	3	1
Poaceae			1	<1			5	2
Thuja plicata					2	<1	497	165
Vaccinium sp.					1	<1	65	22
Picea sp.					1	<1	2	<1
Paxistima myrsinites			41	<1				
Rubus spp.			10	<1				
Abies lasiocarpa			2	<1				
Ericaceae							16	5
Asteraceae							4	1
Pinaceae							2	<1
Juncus ensifolius							1	<1
Graminoid							1	<1
Rubus parviflorus							1	<1
Dicotyledons	7	3	73	<1	1	<1	24	8
Total	14	6	504	6	22	<1	689	229
n	229		9		3		301	
Area (m^2)	2.29		81		27		3.01	

burned subplots.

Epilobium ciliatum germinants were only found in the ICH greenhouse samples. However, some of the *Epilobium* spp. germinants in both burned and unburned field seed banks could have been this species. Similarly, *Ribes lacustre* germinants appear to have been confined to the burned seed bank, but the *Ribes* spp. germinants in the unburned plots and greenhouse samples may have been this species. In addition, the *Rubus* sp. germinants in the burned plots could have been *R. idaeus*.

Paxistima myrsinites, a relatively abundant germinant species, was found only in the burned ICH plots. Conversely, *Vaccinium* spp., *Thuja plicata* and *Picea* sp. germinants were found only in the unburned plots and greenhouse samples, while Ericaceae germinants emerged only from the greenhouse samples.

Sambucus racemosa had the highest number of germinants in five of the burned ICH plots and the same number as unidentified dicotyledons in a sixth. *Rubus idaeus* was the most abundant taxon in two plots while *Paxistima myrsinites* was most common in one plot.

Viola spp., Poaceae, *Ribes lacustre* and *Luzula parviflora* occurred as germinants in the burned ESSF subplots and plots, and in the pre-burn vegetation. Of these taxa, *Viola* spp. and Poaceae were also found in the unburned subplots. *Luzula parviflora* germinated from the greenhouse samples but not the unburned ESSF subplots. No taxa occurred in both the original vegetation and the burned ICH plots and subplots. There were fewer species among germinants than in the pre-burn plant community on both ESSF and ICH sites.

It was not possible to be absolutely certain that any taxon, with the possible exception of *Paxistima myrsinites*, was exclusive to either the burned or the unburned seed banks because unidentified dicotyledons were present in all locations. However, it is unlikely that taxa as numerous as *Mitella* spp., *Thuja plicata* and *Vaccinium* spp. in the unburned seed bank, were absent by chance from the larger area of the burned plots. The fact that *Vaccinium* spp. germinants were found only in the unburned seed banks of both the ICH and the ESSF sites strengthens the evidence that seeds of this taxon did not tolerate burning. Archibold (1989) suggests that the seed coats of *Vaccinium* spp. are too thin and soft to protect seeds from injury during fire.

Paxistima myrsinites germinants had distinct characteristics, even in the cotyledon stage, and therefore it is certain that the species did not germinate from the unburned seed bank. This species may be dependent on fire to break dormancy, or on post-fire conditions for germination. *Paxistima myrsinites* has been found in seed banks by other researchers (Strickler and Edgerton 1976; Kramer and Johnson 1987) but in very small numbers (2 out of 211 germinants and one out of 2406 seeds, respectively). In the former study, some samples were treated with heat, but the authors do not state whether the *Paxistima myrsinites* germinants originated from these or from unheated samples.

The lack of species that were clearly adapted to germinate after fire may have been because, although fire is part of the ecology in the study area, the frequency of natural fires is relatively low. The mean number of years between fires is 150 to

500 years in the ESSF zone and 100 to 350 years in the ICH zone (Parminter 1992). However, the nothing is known about the effect of fire frequency on the evolution of germination requirements of seed bank species in these forests.

The impact of fire on the number of germinant taxa could not be determined since the area involved for the burned and unburned seed banks was different. Also the greenhouse germinants represented the entire thickness of the forest floor whereas germinants in the field plots and subplots probably originated from a limited portion of the profile.

Comparisons between burned and unburned seed banks in the literature are not based on monitoring operational burns and germination in the field. One study showed that artificially burned samples had fewer germinants than unburned control samples but this difference was not significant (Ingersoll and Wilson 1990). Samples collected along a transect from unburned to severely burned areas after a wildfire, yielded the highest mean germinant density from plots subjectively judged to be moderately burned, and the fewest from unburned plots (Archibold 1979). However, the sample size was not equal for each burn severity and there was considerable overlap in germinant densities among plots from different areas, and therefore, these results should be regarded with caution. Also, the criteria used to assign burn severity were not defined.

Two studies have recorded the origin of plant species that grew after logging and burning, including those that germinated from seeds in the field. The density of shrub germinants two years after burning in a *Thuja plicata/Clintonia uniflora* habitat

type in northern Idaho was approximately 6/m^2 (Morgan and Neuenschwander 1988b), slightly more than shrub density (5 germinants/m^2) for the ICH burned plots in the present study. Density values were not presented for germinants in a study of a mixed forest site in southwestern Nova Scotia (Martin 1955).

All of the more abundant germinant taxa from the burned plots and subplots of both the ESSF and ICH sites have been reported in other studies (see Chapter 2, Section 2.3.1.1) of unburned forest floor. *Viola* spp. and *Carex* spp. seed bank germinants have also been observed in the field after logging and slashburning by Martin (1955). Both of these genera were also found in the burned areas of the present study. Three other germinant genera (*Ribes*, *Rubus* and *Sambucus*) were found in both the present study and that of Morgan and Neuenschwander (1988b), but there were no species in common.

The general absence of *Epilobium angustifolium* on the ICH site may have been because the burn was much later than the ESSF site when most of the seeds would have already been dispersed. The ICH site may also have provided a less hospitable seedbed than the ESSF site, due to lack of moisture or some other factor.

Seed densities in temperate forest soils have been described as low compared to the more widely studied seed banks of agricultural weeds and other vegetation types (Roberts 1981). What is not known is how many germinants are needed to make a significant contribution to post-burn vegetation. Nor is it clear in these ecosystems how many seeds must be in the soil to result in enough germinants to replace the parent plants. In fact, the quantity of seeds may not be as important as survival of

germinants, which may depend on chance climatic variations. In the present study, germinants generally did not grow as much over the season in the unburned areas as in the burned areas. This was why fewer germinants were identified to species among the unburned field germinants. It is possible, therefore, that lower germination on the burned areas is compensated for by better growth and survival.

Studies of an arctic tundra site (Racine 1981) and a *Thuja plicata* site in northern Idaho (Morgan and Neuenschwander 1988a) have shown that regeneration from buried seeds is favoured by high severity burns. Morgan and Neuenschwander (1988a) suggest that high severity burns provide a more favourable seedbed by exposing more mineral soil, and are more likely to kill roots and rhizomes thereby reducing vegetative regrowth. However, fire that is severe enough to destroy root systems is not likely to favour regeneration from buried seeds which will be consumed along with the forest floor, unless there is a large number of seeds in the mineral soil.

Several taxa that germinated from the seed bank also regenerate vegetatively after fire or other disturbances. These include *Vaccinium* spp., *Sambucus racemosa*, *Ribes laxiflorum* and *R. lacustre*, *Mitella* spp. and *Rubus parviflorus*. For these species, the seed bank may be a means of diversifying survival techniques to accommodate different disturbances, or simply a chance occurrence not relied upon for regeneration. In the present study, burning appears to have reduced the number of species that regenerate both vegetatively and from seed.

The unburned ESSF subplots may have had a higher germinant

density than the burned subplots because: 1) the temperature reached during the fire was high enough to destroy the seeds near the surface but not high enough to stimulate germination from deeper layers, 2) the species present in the seed bank were particularly sensitive to heat, or 3) the unburned areas provided better germinating conditions (*e.g.* more moisture).

The unburned ICH plots may have had a lower germinant density than the burned plots and subplots because: 1) the thick moss layer inhibited germination by blocking light and/or buffering temperature changes, 2) the area selected for the unburned plots had fewer seeds than the burned to start with, or 3) the severity of the fire, while killing most of the surface seeds, penetrated deeply enough to stimulate germination of the more deeply buried seeds.

3.3.1.2 Germination in the extensive and intensive study areas

Twelve taxa of germinants occurred in the seven ESSFwc2 extensive sites (Table 3.4). The most abundant germinant taxa on these sites were *Epilobium angustifolium* (38%), *Sambucus racemosa* (21%), *Carex* spp. (17%), *Rubus parviflorus* (11%), *Ribes* spp. (4%), and *Ribes lacustre* (2%), accounting for 93% of the germinants. *Epilobium angustifolium* was the only species that occurred in all seven sites while *Sambucus racemosa* occurred in six sites. *Epilobium ciliatum* and *Anaphalis margaritacea* were found in three sites. All other species were found in only one or two sites. *Rubus parviflorus*, with the 4th highest number of germinants, occurred in only three plots of one site.

Germinants belonging to six taxa and unidentified

Table 3.4 Density of germinants (number/m^2) in the extensive plots and intensive burned plots and subplots of the ESSFwc2 study sites.

	Extensive Sites							Intensive Site	
Taxon	1	2	3	4	5	6	7	Plots	Subplots
Epilobium angustifolium	11	2	11	7	19	4	2	4	3
Sambucus racemosa	2	2		23	4	<1	<1	2	1
Anaphalis margaritacea	<1			<1	<1				
Epilobium ciliatum				<1		<1	2	<1	
Carex spp.			14				11	<1	
Ribes lacustre		<1		3				1	1
Luzula parviflora				3				<1	
Ribes spp.		6						<1	
Epilobium sp.			<1						<1
Rubus sp.	<1	<1							
Rubus parviflorus				16					
Rubus idaeus				<1					
Viola spp.								<1	<1
Poaceae								<1	<1
Dicotyledons								<1	
Ribes laxiflorum								<1	
Hieracium spp.								<1	
Cirsium spp.								<1	
Total	13	10	26	53	23	5	16	9	7

dicotyledons were found in the two ICHwk1 extensive sites (Table 3.5). The most abundant germinant taxa were *Sambucus racemosa* (44%), *Rubus idaeus* (31%), *Epilobium angustifolium* (7%), *Ribes* spp. (7%), *Anaphalis margaritacea* (4%), and *Ribes lacustre* (4%) accounting for 97% of the germinants. *Sambucus racemosa* and *Rubus idaeus* were the only species of germinants found in both ICHwk1 sites. All other taxa were confined to one site each.

Germinants of 13 taxa and unidentified dicotyledons occurred in the four ICHmw3 extensive sites (Table 3.5). The most abundant germinant taxa were *Rubus idaeus* (34%), *Sambucus racemosa* (25%), *Paxistima myrsinites* (13%), *Rubus parviflorus* (9%), and *Populus tremuloides* (6%) accounting for 87% of the germinants. No taxon occurred in all the sites but *Paxistima myrsinites*, *Rubus parviflorus*, *Populus tremuloides*, *Rubus* spp. and *Epilobium angustifolium* were found in three of the four sites. Both *Rubus idaeus* and *Sambucus racemosa* germinants were found in two out of the four sites. The remaining species occurred in only one site.

Despite the variation in species composition and biogeoclimatic identification of the extensive sites, several germinant taxa were broadly distributed. *Sambucus racemosa* and *Epilobium angustifolium* germinants occurred in all biogeoclimatic variants and both extensive and intensive sites. *Sambucus racemosa* germinants occurred in most of the extensive sites and all plots of both intensive sites. *Epilobium angustifolium* germinants had the highest abundance and frequency in the intensive and extensive ESSFwc2 sites but relatively low frequency and abundance in both intensive and extensive ICH sites.

Table 3.5 Density of germinants (number/m^2) in the plots of the ICHmw3 and ICHwk1 extensive study sites and in the burned plots and subplots of the intensive ICHwk1 study site.

	Extensive Sites						Intensive Site	
	ICHmw3				ICHwk1		ICHwk1	
Taxon	1	2	3	4	1	2	Plots	Subplots
Epilobium angustifolium	<1	2	<1		1		<1	
Sambucus racemosa	21		<1		7	2	2	
Rubus idaeus	25		5		2	4	<1	<1
Paxistima myrsinites	<1		<1	11			<1	
Anaphalis margaritacea		<1				<1	<1	
Ribes lacustre	<1					<1	<1	<1
Populus tremuloides	2	3	<1					
Rubus sp.	2	1	<1					
Rubus parviflorus	8	<1	<1					
Asteraceae				<1				
Epilobium ciliatum		<1						
Betula paperifera		<1						
Carex spp.	1							
Ribes spp.					1			
Ribes laxiflorum							<1	1
Abies lasiocarpa							<1	
Epilobium spp.							<1	
Poaceae							<1	
Dicotyledons		<1		<1	<1		<1	
Total	59	9	8	12	12	8	4	3

Ribes lacustre germinants occurred in all biogeoclimatic variants and in the plots and subplots of both intensive sites. This species, however, had low presence and abundance among the extensive sites and among plots and subplots of the ICHwk1 intensive site. Only in the intensive ESSFwc2 plots were *Ribes lacustre* germinants relatively abundant with high presence (89%). The intermittent distribution of this species, both within and among sites may reflect the distribution of mature plants.

Rubus idaeus germinants were found almost entirely in ICH sites of both variants, and were abundant with high frequency in both the intensive and extensive plots. Only one germinant of *Rubus idaeus* occurred in the ESSFwc2 extensive sites. *Paxistima myrsinites* was not found in any ESSFwc2 sites. *Carex* spp. germinants were moderately abundant but with low frequency in the ESSFwc2 extensive and intensive plots and sites, and had only three germinants in one ICHmw3 extensive plot. *Luzula parviflora* germinants were found exclusively in the ESSFwc2 extensive and intensive plots, but with low abundance and frequency.

Germinants of all other taxa were either rare or not consistently associated with any of the variants sampled. For example, *Rubus parviflorus* germinants were relatively abundant in the extensive ESSFwc2 and ICHmw3 plots, though with low frequency in the former variant. *Paxistima myrsinites* germinants were relatively frequent in the intensive ICHwk1 and extensive ICHmw3 plots but were not found in the extensive ICHwk1 sites. *Ribes laxiflorum* and Poaceae germinants were found only in the ESSFwc2 and ICHwk1 intensive sites, while *Viola* spp. germinants were found only in the ESSFwc2 intensive plots and subplots. Apart

from *Viola* spp. and *Ribes laxiflorum*, most of the more abundant germinant taxa that emerged in the intensive sites were found in the extensive sites of one or both zones.

3.3.2 **Effects of temperature during the fire, and depth of burn, on seed mortality and germination in the field**

The distribution of forest floor depth of burn (DOB) classes in the subplots of the ESSF and ICH intensive sites, is shown in Figure 3.3. Much more forest floor was consumed on the ICH site than on the ESSF site. For the ESSF site mean DOB was 0.3 cm ($\pm$ 0.04 S.E.) and maximum DOB was 2.7 cm, while for the ICH site mean DOB was 1.5 cm ($\pm$ 0.07 S.E.) and maximum DOB was 5.9 cm. Over one-third (37%) of the ESSF subplots had 0 cm DOB, and 84% had less than 1 cm DOB. Only 3% of the ICH subplots had 0 cm DOB, while 67% had > 1 cm DOB. The number of subplots per DOB class decreased sharply with increasing DOB on the ESSF site, whereas on the ICH site the number of subplots with DOB between 1 and 2 cm exceeded the number of subplots with < 1 cm DOB.

In the ESSF plots, average DOB ranged from 0.2 to 0.8 cm. mean DOB was $\leq$ 0.5 cm in all but one plot. Mean DOB for the ICH plots ranged from 0.6 to 2.7 cm. Six of the ICH plots had DOB between 1 and 2 cm, and only one plot had a mean DOB < 1 cm.

Seed consumption was estimated to be much higher on the ICH site even though the estimated total number of seeds in the forest floor of ESSF subplots was greater. Approximately 10% of the total seeds (1851) in the ESSF subplots were consumed along with the forest floor. Of the total seeds (525) estimated to occur in the forest floor of the burned ICH subplots, 71% were

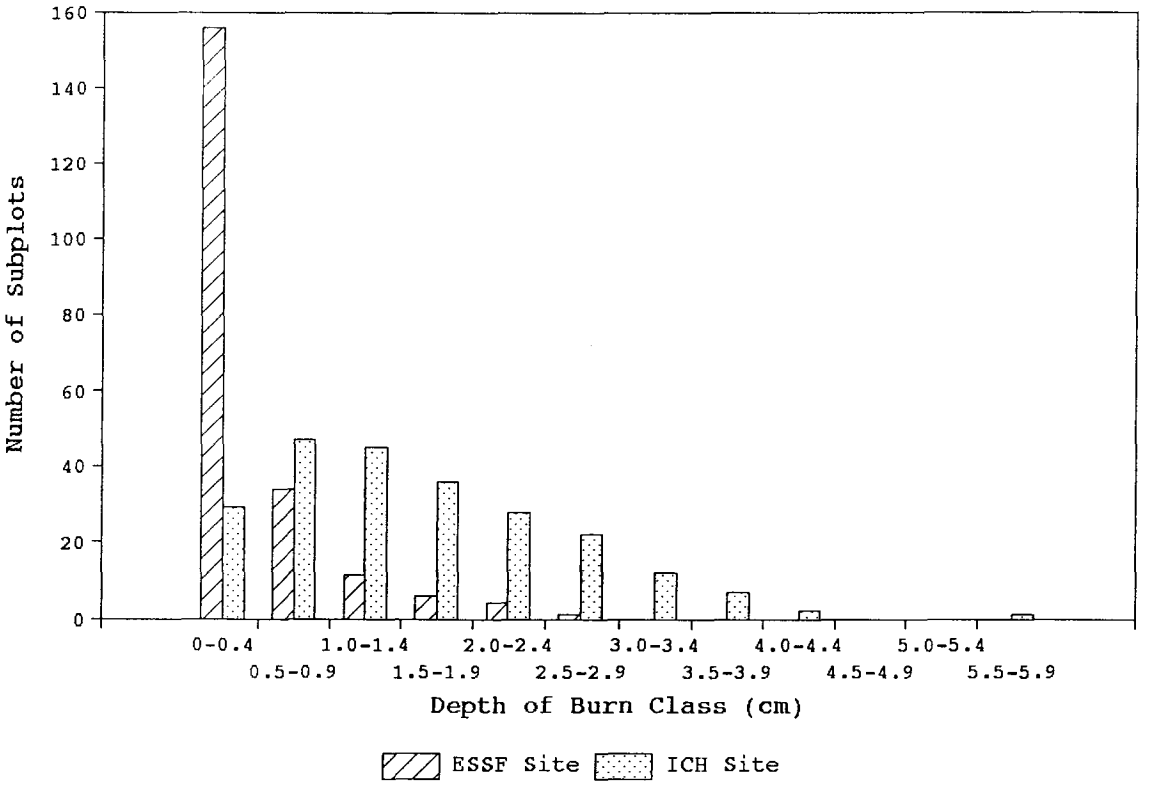

Figure 3.3 Number of subplots in 0.5 cm depth of burn classes from the ESSF and ICH intensive sites.

consumed. Most of the seeds consumed were from the 0-1 cm depth class (84 and 87% in the ESSF and ICH, respectively).

The fact that more seeds were consumed on the ICH site was a function of both the vertical distribution of the seeds and the amount of forest floor consumed. A much greater proportion of seeds occurred in the top 2 cm of the ICH forest floor compared to that of the ESSF (92 and 55%, respectively) and a much higher volume of forest floor was consumed on the ICH site than on the ESSF site.

The number of seeds predicted to be present in the post-burn 0-1 cm of forest floor in the burned subplots was much greater than the actual number of germinants in the subplots. Over all ESSF subplots only 9% of the 522 predicted seeds germinated. In the ICH subplots 13% of the predicted 111 seeds germinated. When these results were broken down by subplots within DOB classes, all ESSF subplots and most ICH subplots had many fewer germinants than were predicted. In ICH subplots with DOB of 1.7 and 1.8 cm, the number of germinants was equal to the number predicted, while in subplots with a 1.9 cm DOB germinants were higher than predicted. These results for the ICH are, however, based on very few germinants (two, one and three, respectively) and therefore could reflect a chance occurrence of seeds rather than a positive response to DOB. In addition, three of the germinants were never identified so it was not possible to assess whether these originated from buried seed or from seed blown onto the site after the burn.

The comparison between remaining seeds and actual germinants is tentative because germinants may actually have originated from

deeper than 1 cm from the post burn surface. Little is known about the depth from which seeds of any species can germinate (Parker *et al.* 1989) including the species found in this study. Results of the few existing studies indicate that maximum germination depth varies widely among species and plant communities from 2-4 cm for desert herbs and shrubs (Kemp 1989), to 8 cm in tropical forest trees (Maun and Riach 1981), to 13.5 cm for an agricultural weed (Colosi *et al.* 1988). *Luzula pilosa* has been reported to germinate from a 2 cm depth (Kujala 1926 cited in Granstrom 1982) but there is no information on *L. parviflora* which germinated in this study.

The low rate of germination compared to the predicted number of seeds in the post-burn 0-1 cm of forest floor probably indicates that seeds in the unconsumed forest floor were also killed by the fire. Whether additional seed mortality was caused by exposure to lethal heating during the fire or by other factors cannot be determined from the results of this study. Poor germination may also have been the result of unfavourable germination conditions after burning.

Most burned ESSF subplots with germinants had DOB of < 0.7 cm, although germinants were also found in two subplots with 1.8 cm and 2.4 cm DOB. However, the germinants in these two subplots were *Epilobium* spp., which could have germinated from seeds that were blown in after the burn, and not from the seed bank. Depth of burn was not significantly correlated with either the total number of germinants in the subplots (r_S = -0.04, p = 0.59), or the total number of surviving germinants in the plots (Table 3.6). None of the germinant taxa was significantly correlated

Table 3.6 Spearman rank correlation coefficients (r_s) for the number of surviving germinants versus depth of burn in the plots of the ESSF intensive site, for the most abundant taxa and total germinants.

Taxon	r_s	
Sambucus racemosa	0.36	ns
Ribes lacustre	-0.43	ns
Viola spp.	-0.12	ns
Epilobium ciliatum	0.06	ns
Carex spp.	0.12	ns
Total Germinants	-0.21	ns

ns = not significant at p=0.05
n = 9 plots

with mean DOB in the plots (Table 3.6).

Germinants were not present in any burned ICH subplots that had DOB > 2 cm. The occurrence of germinants was not uniform as many 0.1 DOB classes had no germinants and no more than 27% of the subplots in any one class had germinants. Except for one DOB class (1.8 cm) most subplots with germinants occurred in classes that had relatively high total numbers of subplots. However, several DOB classes with high numbers of subplots had no germinants in them so the occurrence of germinants was not simply a function of the larger sample area. Depth of burn was not significantly correlated with the total number of germinants in either subplots (r_s = -0.10, p = 0.12) or plots (Table 3.7). Mean DOB was not significantly correlated with the number of germinants per plot for any of the taxa individually (Table 3.7).

Temperatures at depths of 3 and 4 cm did not exceed 100°C during the 1990 ESSF burn. There was a negative relationship between the length of time temperatures at 1 cm exceeded 60, 70, 80 and 100°C and the mean depth of burn during the 1990 ESSF fire. This correlation was only significant for time exceeding 70°C (Table 3.8). For other depths, correlation coefficients were generally positive but were not significant. Maximum temperatures reached during the burn decreased with increasing forest floor depth at each measurement location (Table 3.9). The correlation between maximum temperature reached during the slashburn and mean depth of burn was not significant at any depth (Table 3.9).

Temperatures exceeding 100°C were recorded during the 1989 ICH burn at 1 cm depth in all but one out of the 12 locations, at 2 cm depth in nine locations, and at 4 cm depth in six locations.

Table 3.7 Spearman rank correlation coefficients (r_s) for the number of germinants versus depth of burn in the plots of the ICH intensive site, for the most abundant taxa and total germinants.

Taxon	r_s	
Sambucus racemosa	0.52	ns
Rubus idaeus	0.40	ns
Ribes laxiflorum	-0.34	ns
Paxistima myrsinites	-0.16	ns
Ribes spp.	-0.49	ns
Ribes lacustre	0.33	ns
Total Germinants	-0.50	ns

ns = not significant at p=0.05
n = 9 plots

Table 3.8 Correlation coefficients (r) for the number of minutes temperatures exceeded 60, 70, 80 and 100°C during the 1990 ESSF burn, versus mean depth of burn.

	Depth (cm)			
	1	2	3	4
>100°C	-0.81	0.59		
>80°C	-0.87	0.43	0.11	
>70°C	-0.96*	0.20	0.24	0.34
>60°C	-0.87	0.10	-0.32	0.78

* significant: p = 0.04
All other values are not significant at p = 0.05.
n = 4 locations

Table 3.9 Correlation coefficients (*r*) for maximum temperatures (^{o}C) reached during the 1990 ESSF burn versus mean depth of burn, by location and depth.

	Location						
Depth (cm)	1	2	3	4	Mean	*r*	p
0	573.1						
1	546.2	500.4	778.0	649.4	618.5	-0.72	0.28
2	503.6	270.0	102.1	232.0	276.9	0.78	0.22
3	85.0	76.8	68.7	86.9	79.4	0.09	0.91
4	63.8	72.1	44.3	52.8	58.3	0.74	0.26
6	27.6	31.2	28.1	28.1	28.8	0.23	0.77
10	14.9		7.9	17.7	13.5		
Mean DOB	1.9	1.6	1.0	0.7	1.3		

The length of time over 60, 70 or 100°C was not significantly correlated with the mean depth of burn at any depth (Table 3.10). Correlation coefficients for the 1 cm depth were just slightly less than the critical value of r ($0.10 > p > 0.05$) and all were positive.

No consistent relationship was demonstrated by these results, between either maximum temperatures or duration of elevated temperatures during burning, and depth of burn. However, the forest floor of the ICH site was exposed to temperatures exceeding 100°C for longer periods of time at deeper locations in the profile than was the ESSF site burned in 1990, and also had a higher overall mean DOB. The intensive ESSF site (burned in 1989) had the lowest mean DOB of the three sites and may, therefore, have been exposed to lower temperatures than either the ICH site or the ESSF site burned in 1990.

The poor relationship between the number of germinants and DOB may have been because the range of DOB was too narrow to be biologically significant, especially in the plots. Alternatively, variation in initial species composition, numbers and distribution of seeds, combined with variation in DOB, may have obscured species-specific sensitivity to fire. So few germinants occurred in the subplots, especially on the ICH site, that any effect of DOB would have been difficult to demonstrate. DOB was useful primarily as a means to estimate seed mortality through forest floor consumption.

The relative lack of correlation between DOB and either germination or the magnitude and duration of elevated temperatures during fire suggests that DOB may not be a reliable

Table 3.10 Correlation coefficients (*r*) for the number of minutes temperatures exceeded 60, 70 and 100°C during the 1989 ICH burn, versus mean depth of burn.

	Depth (cm)		
	1	2	4
>100°C	0.56	0.36	0.09
>70°C	0.56	0.36	0.08
>60°C	0.56	0.34	0.17

None of the values were significant at p = 0.05
n = 12 locations

indicator of soil heating. It is likely that the sample size used in this study was too small to base a model of soil heating on. This does not mean, however, that temperature did not affect germination. On both sites there appeared to be a level of DOB beyond which no germination took place (0.6 cm and 1.9 cm in the ESSF and ICH, respectively). This may indicate a threshold level of heating for buried seeds, since the greenhouse germination demonstrated that seeds were present deeper in the profile.

Although the specific heat tolerances of most species of germinants recorded by this study are not known, other researchers have demonstrated that seeds of many species tolerate, and in some cases are stimulated to germinate by, exposure to a wide range of elevated temperature/time treatments (Stone and Juhren 1951; Went *et al.* 1952; Floyd 1966). Pratt *et al.* (1984) found that the germination of *Epilobium ciliatum* (formerly *watsonii*) seeds was the same from samples heated to 75 and 100^{o}C for 20 minutes. Seeds of various other species heated to 100^{o}C for as little as five minutes (Stone and Juhren 1951; Went *et al.* 1952; Daubenmire 1968; Munoz and Fuentes 1989) and as much as 400 minutes (Floyd 1966) have germinated.

Results from this and other studies (summarized in Wells *et al.* 1979) show that temperatures during burns can reach from 65^{o}C to 545^{o}C at 1 cm depth and from a slight rise to > 100^{o}C at 5 cm depth. Few studies, however, have determined the duration of exposure to various temperatures or distinguished between forest floor and mineral soil. For these reasons, direct comparison with the present study cannot be made. Two studies in which forest floor samples were heated for 20 minutes at 60, 80 and 100^{o}C

(Strickler and Edgerton 1976), and 75 and 100°C (Pratt *et al.* 1984) had the fewest germinants from the 100°C treatment although the differences were not significant.

The length of time seeds were heated in other studies was generally 20 minutes or less. In the present study, the unconsumed forest floor was exposed to temperatures of > 100°C for either similar or less time during the 1990 ESSF burn but for much longer during the 1989 ICH burn. Experimental heat treatments also do not mimic the patterns of heating that are found under natural conditions. In the field, buried seeds are subjected to a continuum of temperature rise and fall. Thus seeds that experience some minutes at 70°C may also experience temperatures of 100°C or more during the fire.

3.3.3 **Effects of burning and shade on post-burn soil temperature and germination**

3.3.3.1 Temperature

During most days the soil temperature was lowest from 5:00 to 7:00 AM and reached a peak in the afternoon (usually between noon and 3:00 PM on the ESSF site and 3:00 to 5:00 PM on the ICH site) (Figures 3.4, 3.5). On both sites, hourly temperatures during the hottest part of the day were generally higher at unshaded locations than at shaded locations, in both the burned and the unburned areas at all depths. Burned areas had higher temperatures than unburned areas in both shaded and unshaded treatments of the ESSF site (Figure 3.4). On the ICH site, however, the burned location had higher temperatures than the unburned location in the shaded area but lower temperatures in

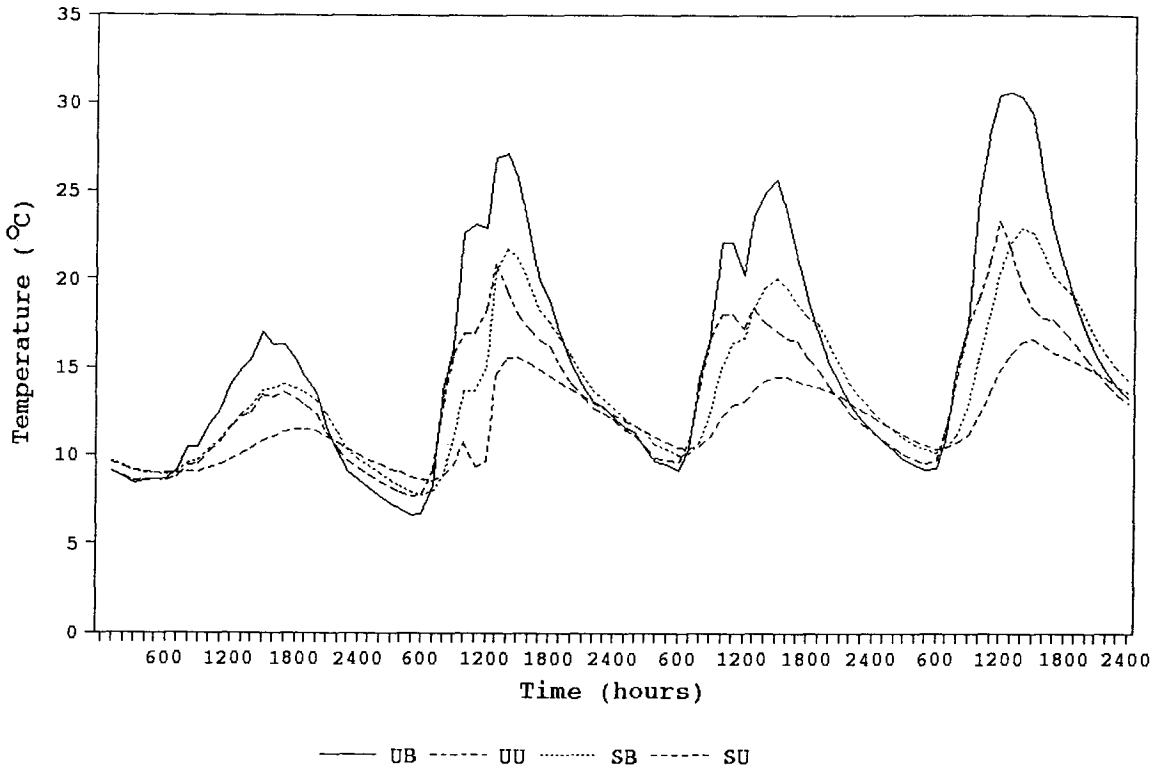

Figure 3.4 Typical pattern of hourly mean temperatures (^{o}C) over four days (July 7 - 10, 1990) at 1 cm depth in the forest floor of the four shade and burn treatments in the ESSF intensive study site. UB = unshaded/burned, UU = unshaded/unburned, SB = shaded/burned, SU = shaded/unburned.

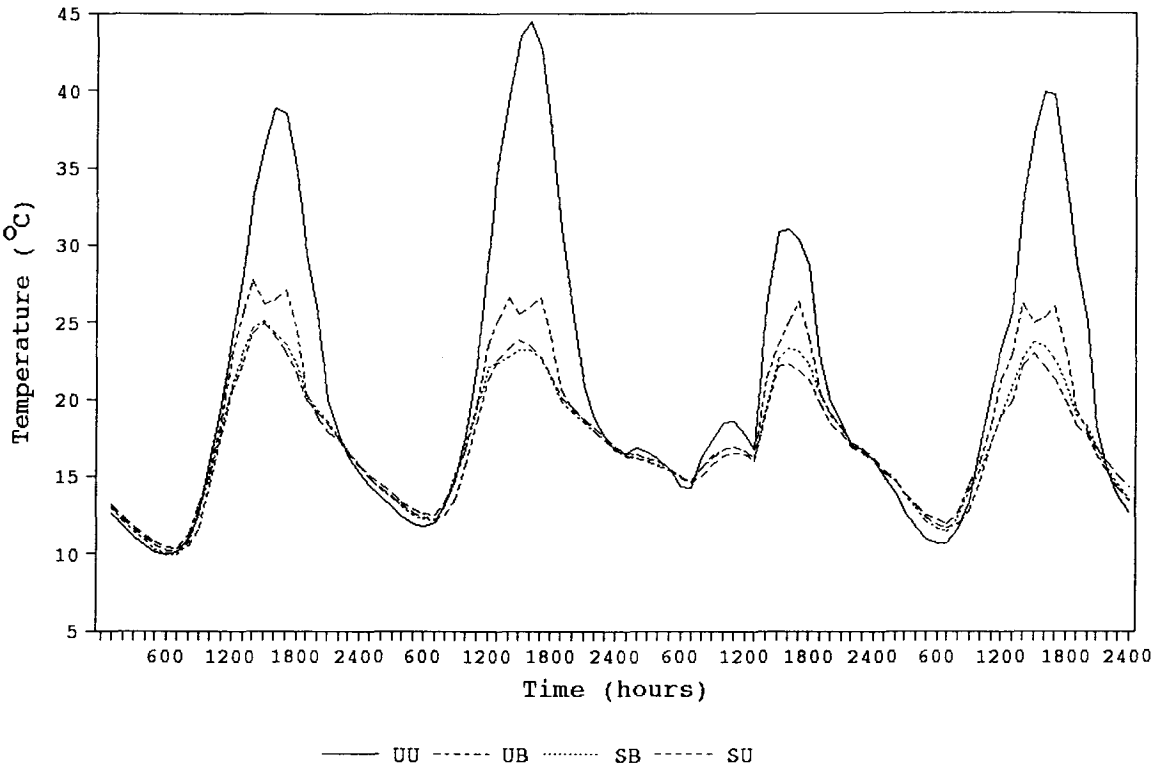

Figure 3.5 Typical pattern of hourly mean temperatures (^{o}C) over four days (July 10 - 13, 1990) at 1 cm depth in the forest floor of the four shade and burn treatments in the ICH intensive study site. UU = unshaded/unburned, UB = unshaded/burned, SB = shaded/burned, SU = shaded/unburned.

the unshaded area (Figure 3.5). On the ESSF site, unshaded/ unburned temperatures were often similar to shaded/burned temperatures, while on the ICH site shaded/unburned temperatures often overlapped unshaded/burned temperatures, especially at the 2 cm depth.

The difference between maximum and minimum temperatures (the range) varied considerably from day to day and from location to location (Figures 3.6, 3.7). The daily temperature range was generally greater in unshaded than in shaded locations, and on hotter days. Day-to-day fluctuation of maximum temperatures was also greater in unshaded than in shaded locations.

Minimum temperatures fluctuated from day-to-day much less than the daily maximum temperatures and the range of minima was much narrower than the range of maxima for each location, over the growing season. Minimum temperatures were also much more similar among locations and depths than maximum temperatures. Maximum temperatures were, therefore, largely responsible for differences in mean temperatures among locations and depths. This was probably because the minima generally occurred during darkness or before sunrise, when shading and surface colour had little or no influence on temperature.

Over the season, the highest temperatures were reached during August 10th to 20th for the ESSF site (Figure 3.8) and August 5th to 15th for the ICH site (Figure 3.9). All locations on both sites showed a general increase in average temperatures over the whole season but the trend was most pronounced at the locations with the highest temperatures (unshaded/burned on the ESSF and unshaded/unburned on the ICH site) (Figures 3.8, 3.9).

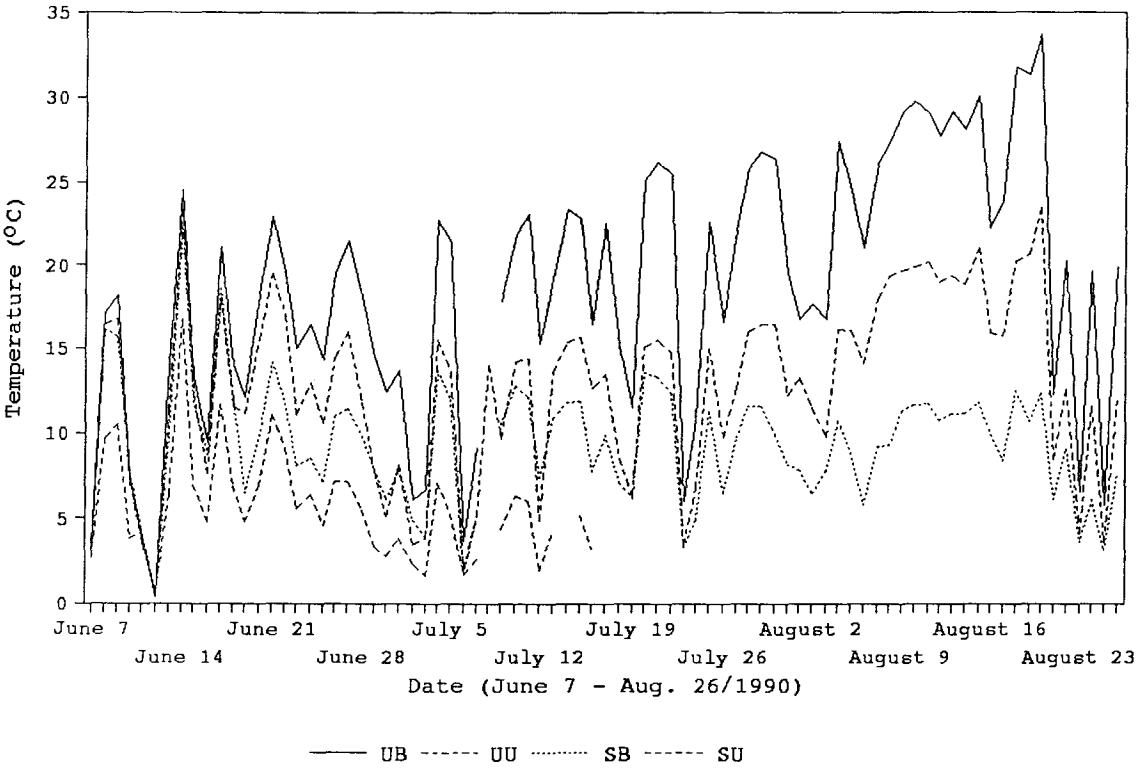

Figure 3.6 Daily mean range (maximum - minimum) of temperatures (^{o}C) at 1 cm depth in the forest floor of the four shade and burn treatments in the ESSF intensive site during the 1990 growing season. UB = unshaded/burned, UU = unshaded/unburned, SB = shaded/burned, SU = shaded/unburned.

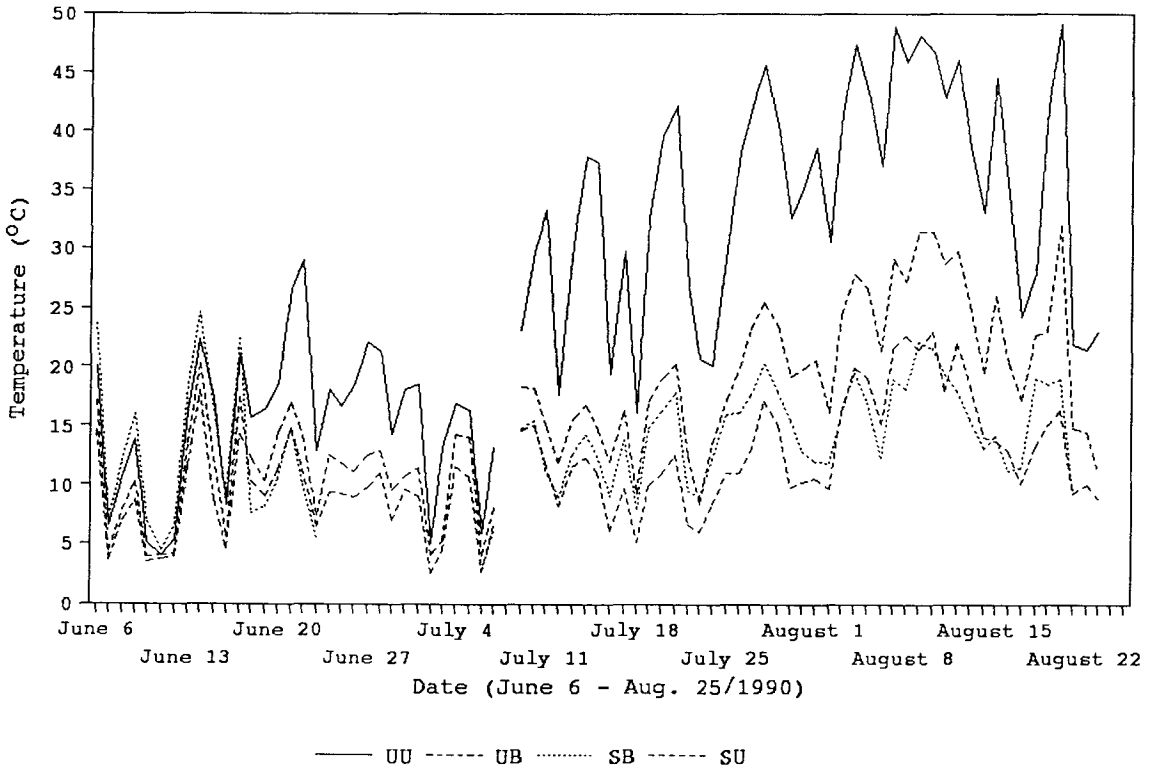

Figure 3.7 Daily mean range (maximum - minimum) of temperatures (^{o}C) at 1 cm depth in the forest floor of the four shade and burn treatments in the ICH intensive site during the 1990 growing season. UU = unshaded/unburned, UB = unshaded/burned, SB = shaded/burned, SU = shaded/unburned.

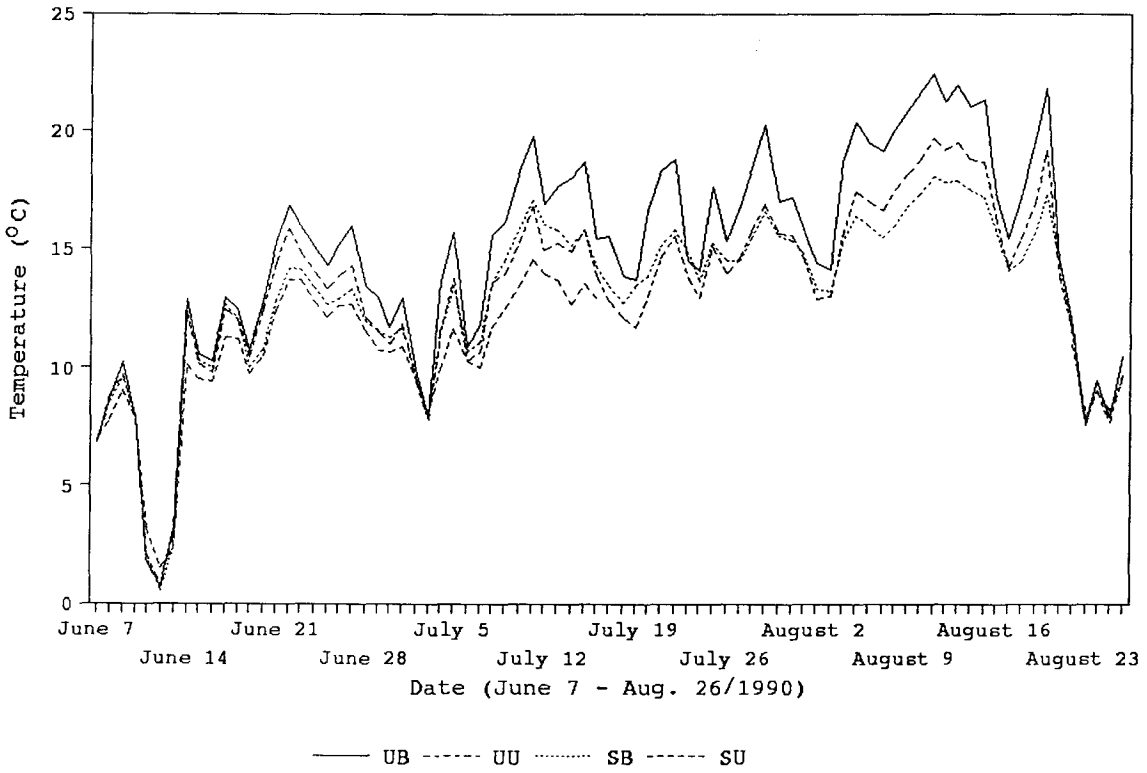

Figure 3.8 Daily mean temperatures (°C) recorded at 1 cm depth in the forest floor of the four shade and burn treatments in the ESSF intensive site during the 1990 growing season. UB = unshaded/burned, UU = unshaded/unburned, SB = shaded/burned, SU = shaded/unburned.

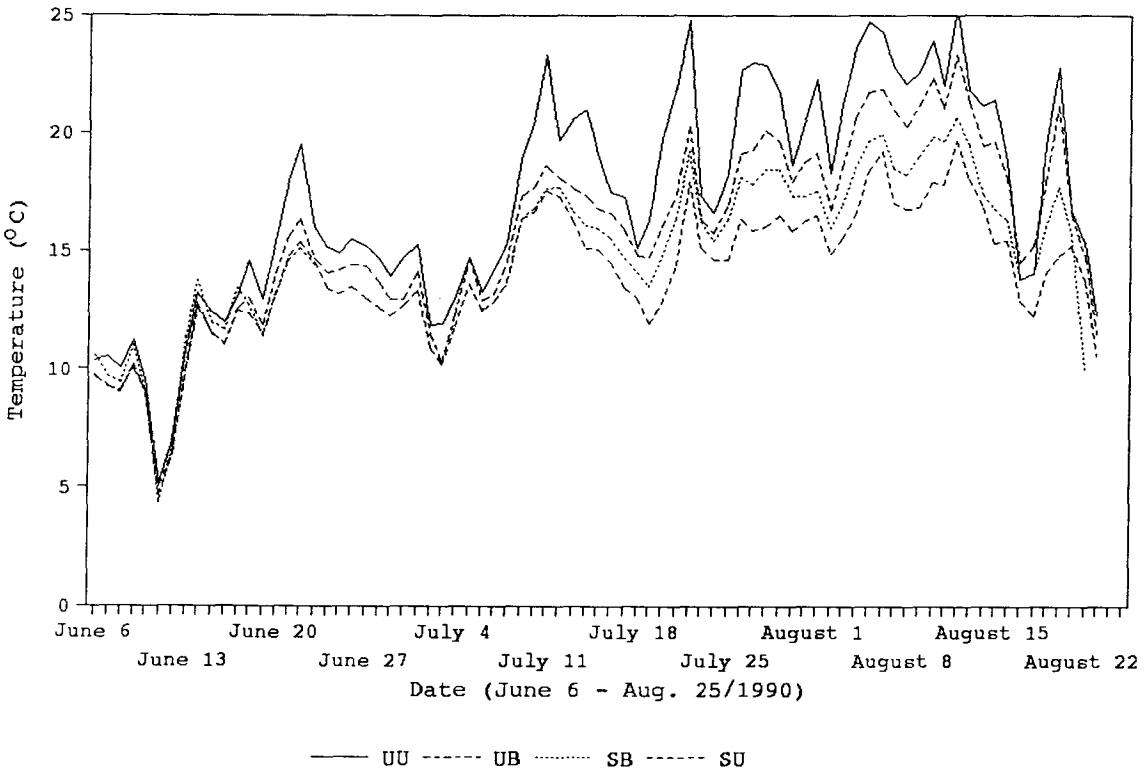

Figure 3.9 Daily mean temperatures (°C) recorded at 1 cm depth in the forest floor of the four shade and burn treatments in the ICH intensive site during the 1990 growing season. UU = unshaded/ unburned, UB = unshaded/burned, SB = shaded/ burned, SU = shaded/ unburned.

Mean temperatures for the whole season in the ESSF site were highest for the unshaded/burned treatment, followed by the unshaded/unburned, shaded/burned and shaded/unburned treatments (Table 3.11). On the ICH site, the unshaded/unburned location had the highest mean temperatures over the whole season followed by unshaded/burned, shaded/burned and shaded/unburned treatments (Table 3.12).

At both sites, hourly mean temperatures decreased with increasing depth during the hottest part of the day but reversed during the coolest period. For this reason, the range of temperatures decreased with increasing depth. The daily pattern of temperature at the 4 cm depth tended to lag behind that of the 1 and 2 cm depths by one to two hours.

The only exception to the above pattern occurred in the shaded/unburned location of the ESSF site, where the maximum temperature was higher at the 2 cm depth than at the 1 cm depth. Although there is a slight possibility the leads were incorrectly attached to the datalogger, it is more likely that the thermocouple was not working properly, since it appeared to malfunction most of the summer.

Higher temperatures were expected to occur in burned areas than in unburned areas, in unshaded than in shaded areas, and at locations closer to the surface compared to those deeper in the profile (Smith and James 1978; Wells *et al.* 1979). The dark surface of burned forest floor can result in higher temperatures through increased heat absorption. Shaded surfaces are cooler because they are protected from insolation (Wells *et al.* 1979). Unshaded soil can reach temperatures as high as 60 to 70^{o}C due to

Table 3.11 Maximum, mean and minimum temperatures (^{o}C) recorded from June 19 to August 26, 1990, in the four shade and burn treatments on the ESSF intensive site.

	1 cm			2 cm			4 cm		
Treatment	max	mean	min	max	mean	min	max	mean	min
UB	43.9	16.1	2.4	39.7	15.4	4.3	27.0	14.6	5.1
UU	34.0	14.3	4.7	26.6	13.8	5.7	25.7	13.7	5.9
SB	24.8	14.0	4.9	21.8	13.8	5.5	19.6	13.5	6.0
SU	18.5	11.8	6.3	22.6	12.9	6.0	19.1	12.3	6.4

UB = unshaded/burned, UU = unshaded/unburned, SB = shaded/burned, SU = shaded/unburned

Table 3.12 Maximum, mean and minimum temperatures (^{o}C) recorded from June 18, to August 25, 1990, in the four shade and burn treatments on the ICH intensive site.

	1 cm			2 cm			4 cm		
Treatment	max	mean	min	max	mean	min	max	mean	min
UU	57.4	18.5	5.0	45.8	17.4	6.5			
UB	43.4	16.9	5.8	27.0	15.7	7.1			
SB	32.7	16.4	6.8	25.6	15.1	6.8	21.1	14.9	7.9
SU	34.4	14.8	6.5	30.9	14.6	6.8	21.0	14.2	8.3

UU = unshaded/unburned, UB = unshaded/burned, SB = shaded/burned, SU = shaded/unburned

insolation, which can cause mortality in weed seeds after exposures of several days (Egley 1990). Once vegetation grows enough to shade the soil surface, the effects of burning on temperature may be neutralized, even within the first growing season (Daubenmire 1968; Smith and James 1978).

Temperatures recorded on the ESSF site were consistent with the expected patterns in the shade and burn treatments. The fact that the unburned/unshaded location had the highest temperatures on the ICH site is difficult to explain. This could have been an anomalous result, brought about by particular conditions where the thermocouple was located. Alternatively, the temperatures could have been within the normal variation that would have been detected with sufficient replication of the measurements.

Mean seasonal temperatures were generally higher on the ICH site than on the ESSF site, although there was some overlap between the ESSF location with the highest temperature (unshaded/burned) and the ICH location with the lowest temperature (shaded/unburned). This may have been due, at least in part, because of moister soils in the ESSF site and, on the unburned areas, more vegetation cover.

3.3.3.2 Germination

The ratio of observed germinants per treatment was significantly different from the expected ratio for burned versus unburned subplots in the intensive ESSF site (Table 3.13). There was a higher than expected frequency of germinants in the unburned subplots and a lower than expected frequency of germinants in the burned subplots (Table 3.13). In fact the

Table 3.13 Frequency of subplots, and observed and expected frequencies of germinants in the burned versus unburned subplots of the ESSF intensive study site. Results of the 'goodness of fit' analysis are presented.

	Burned	Unburned	Total
Number of Subplots	225	75	300
Observed No. of Germinants	49	128	177
Expected No. of Germinants	133	44	
Calculated chi-squared statistic			208.83***

significant: *** = $p \leq 0.001$

observed ratio was almost the reverse of that expected.

Within both the burned and unburned areas on the intensive ESSF site, the frequency of germinants was higher than expected in the shaded subplots and lower than expected in the unshaded subplots (Table 3.14). There was a significant difference between the observed and expected ratio of germinants in shaded versus unshaded subplots of the burned treatment but not in the unburned treatment.

On the ESSF site, burning appears to have had a greater influence on germinant density than did shading. The relative difference between densities in the burned subplots versus those in the unburned subplots was much greater than the difference between densities in shaded and unshaded subplots within the burned and unburned treatments (Table 3.15).

Results from the ESSF site showed that the lowest germinant density was in the unshaded/burned subplots (Table 3.15) which also had the highest mean temperature. Conversely, the shaded/ unburned subplots with the lowest mean temperature had the highest density of germinants. Of the remaining treatments, the unshaded/unburned subplots had a much higher germinant density than the shaded/burned subplots, even though their mean temperatures were similar (Tables 3.11, 3.15).

Neither the shaded/unburned nor the unshaded/unburned ICH subplots had any germinants, even though these two treatments had the lowest and highest mean temperatures, respectively (Tables 3.12, 3.16). The two burned treatments had similar mean temperatures and both had low densities of germinants. The unshaded/burned subplots had a slightly higher temperature and

Table 3.14 Frequency of subplots, and observed and expected frequencies of germinants in shaded versus unshaded subplots within burned and unburned areas of the intensive ESSF field study site. Results of the 'goodness of fit' analysis are presented.

		Shaded	Unshaded	Total
Burned	Number of Subplots	45	180	225
	Observed No. of Germinants	19	30	49
	Expected No. of Germinants	10	39	
	Calculated chi-squared statistic			9.65*
Unburned	Number of Subplots	15	60	75
	Observed No. of Germinants	33	95	128
	Expected No. of Germinants	26	102	
	Calculated chi-squared statistic			2.32ns

significance: ns = not significant ($p \geq 0.05$), * = $0.005 \leq p > 0.001$.

Table 3.15 Density (number/m^2) of germinants in the four shade and burn treatments of the intensive ESSF and ICH field study sites.

	Burned		Unburned	
	Shaded	Unshaded	Shaded	Unshaded
ESSF Site	42	17	220	158
ICH Site	4	7	-	-

Table 3.16 Frequency of subplots and germinants in the four shade and burn treatments of the ICH intensive study site.

	Burned		Unburned	
	Shaded	Unshaded	Shaded	Unshaded
Number of subplots	67	162	3	72
Number of germinants	3	11	0	0

also a higher density of germinants (Table 3.15).

Results from both these sites suggest that the differences in germinant density were not directly related to differences in the temperature environment of the forest floor among the shade and burn treatments. Other factors, such as differences in soil moisture or chemistry that resulted from burning and shading, may have affected germination, either alone or in combination. Temperature may still have been important but could have been interacting with other variables which were not measured in this study.

The actual differences between the mean temperatures were not very great but that was because they were averaged over the whole season. Since the optimal germination conditions for the germinant species encountered in this study are not known, it is not possible to assess whether these temperature differences could have had a significant effect.

Results from other studies that germinated soil samples under controlled conditions are, like this study, inconsistent. Ingersoll and Wilson (1990) found that neither shading nor burning had a significant effect on germination from blocks of forest soil. Shade generally decreased germination from soil samples but the effect was significant only at the highest shade levels (Pratt *et al.* 1984). In another study, shade significantly reduced germination of *Epilobium ciliatum* (*watsonii*), but *Mitella* sp. emerged almost exclusively from shaded samples (Strickler and Edgerton 1976). However, there were too few *Mitella* sp. germinants to test whether the latter result was significant.

Seeds of some species that form soil seed banks are

stimulated to germinate in the dark by diurnal fluctuations in temperature (Thompson and Grime 1983). Fluctuations in temperature decrease with depth and shading, which could function as a means to prevent seeds from germinating when they are too deep to reach the surface, or where high shade levels would be detrimental to growth and survival of germinants (Thompson and Grime 1983). This does not appear to be the case for the seed bank species encountered in the present study.

3.4 **Conclusions**

Burning did not have a consistent effect on field germination. On the ESSF site burning resulted in fewer germinants while on the ICH site there were more field germinants in the burned area than in the unburned area. Differences between these two sites in burn severity, initial abundance and distribution of seeds, moss cover on the unburned areas and soil moisture regime, may have affected the germination response on burned versus unburned areas.

Germinants grew faster and larger on the burned areas than on the unburned areas of both the ESSF and ICH intensive study sites. This increased growth may result in better survival which could counteract the lower numbers of germinants in burned than in unburned areas on, for example, the ESSF intensive site.

Only one germinant species appeared to have been favoured by burning (*Paxistima myrsinites* in the ICH site). Several, however, were absent from the burned areas (*e.g. Mitella* spp., *Vaccinium* spp.). The fact that only one taxon may have depended on fire to germinate is consistent with the relatively low frequency of

natural fire in the study area.

The occurrence of germinant species was inconsistent both among plots within sites and among sites within variants and zones. At the smaller scale this variation probably reflects the highly clustered nature of buried seeds combined with variation in microtopography and fire severity. At the larger scale, differences in seed production, burn severity and vegetation history were likely responsible for between-site variation.

Most of the abundant germinant taxa encountered in the intensive sites were also found in some of the extensive sites. However, only *Epilobium angustifolium* and *Sambucus racemosa* were found on all sites and the former probably seeded in primarily from off-site sources. Several other taxa were found in all three variants sampled but in fewer sites. Few of the more abundant taxa were confined to one variant or zone. Of these, *Luzula parviflora* was found only in the ESSFwc2 sites, while *Paxistima myrsinites* was confined to the ICH zone, mainly in the ICHmw3 sites.

The concentration of seeds in the upper 3 cm of the forest floor probably resulted in high seed mortality through combustion of the forest floor, especially on the ICH site. However, the number of germinants that occurred in the burned area was a relatively small percentage of what was estimated to remain in the post burn 0-1 cm of the forest floor, indicating that either 1) seeds in the remaining forest floor were killed by the fire or 2) post-burn conditions were unfavourable to germination.

It was not possible to distinguish between these two possibilities because no relationship was established between

depth of burn and either 1) the magnitude or duration of elevated soil temperatures during the burn, or 2) the number of germinants after the burn. A larger sample size and the inclusion of other important factors, such as soil moisture and texture, would be required to construct a model of soil heating.

The fact that there appeared to be a threshold depth of burn beyond which no germination occurred on both sites, suggests that lethal temperatures during the fire could have been responsible for the lack of germination. The length of exposure to relatively high temperatures in this study was within the range that other research has shown to be lethal to seeds of some species, but not to others. Not enough is known about the heat tolerances of seed bank species found in this study to assess the potential for seed mortality.

In the post-burn environment, burning appears to have affected germination more than did shading. It was not possible to determine whether this difference was the result of differences in soil temperatures or some other factor. The fact that shading had a much more important influence on soil temperature than burning, suggests that temperature was not of primary importance to germination. However, since temperature measurements were not replicated and not measured where germination was being monitored, there was no direct measurement of the relationship between these two factors. Knowledge of the effect of different temperature regimes on germination of species in the seed bank would be necessary to determine whether the differences in temperature recorded in this study could have affected germination.

CHAPTER 4 CONCLUSIONS AND RECOMMENDATIONS

4.1 Conclusions

4.1.1 The seed bank

The density of germinants, number of taxa and variation in germinant numbers among samples, appeared to be similar to other greenhouse germination studies of northern temperate forest soils, despite a wide variation in sampling methodology. No genus was unique to this study, although not all germinant species have been found in other studies.

Greenhouse germination appeared to represent the total numbers and species composition of the more abundant seed bank taxa. Taxa that were unique to either the greenhouse samples or the field were relatively rare. Germinant density was much higher in the 0-1 cm depth class of the greenhouse samples than in the field plots and subplots. Therefore, greenhouse germination was not an accurate predictor of field germination.

Results indicate that moist ESSF sites have a relatively large number of buried seeds in the forest floor, many of which will germinate after logging. Soil seed banks did not appear to be an important source of new plants of any species on mesic ICH sites. Site productivity, vegetation history and stand structure, are probably more important than altitude in determining the extent of the buried seed population.

Greenhouse germinants were generally poorly dispersed and were unevenly distributed within the samples in which they occurred. The degree of dispersion and clustering varied greatly among the germinant taxa and was not related to germinant abundance.

Increasing sample size probably increases the precision with which seed numbers are estimated, but between-sample variation is not a good measure of that precision. This is because seed distribution is inherently clustered.

Patterns of vertical distribution represents individual clusters of seeds located at different depths in different samples rather than the same pattern in each sample. These patterns can be highly skewed by large clusters of germinants in one or two samples. Therefore, relatively large sample sizes are required to assess both vertical and horizontal distribution of buried seeds. Layers must also be thin enough to provide good resolution of vertical distribution patterns.

The location of particular germinant species in the profile may indicate when in the successional cycle a species was deposited. However, nothing is known about the seed-burial mechanisms on these sites and therefore it cannot be concluded that there is a relationship between vertical distribution and seed age.

Both mature-forest and early successional taxa were among the seed bank germinants from both sites. Seed banks of mature-forest species are likely maintained through periodic, small disturbances that create gaps in the forest which stimulate seed production. The dense, closed canopy of some forest plantations could lead to a loss or reduction of species that rely on gaps to maintain seed reserves.

The higher densities of germinants found in the greenhouse than in the field may have been due to one or more of: 1) differences in the temperature regime between greenhouse and

field environments, 2) reduced daylength in the greenhouse, 3) lack of moisture in the ICH field site, 4) splitting of greenhouse samples or 5) the longer period and greater frequency of germination monitoring in the greenhouse.

Seeds germinated under a wide variety of temperature conditions in both the greenhouse and the field. The evolution of narrow temperature requirements for germination is unlikely to occur in an temperature environment that is highly unpredictable. Therefore, it is probable that temperature requirements were met for most or all taxa present in the seed bank.

4.1.2 **Effects of fire on the seed bank**

Burned areas had fewer germinants than unburned areas on the ESSF site but the reverse occurred on the ICH site. The different germination response on these two sites may have resulted from differences in burn severity, initial abundance and distribution of seeds, moss cover on the unburned areas and soil moisture regime.

Germinants appeared to grow larger during the summer on the burned areas than on the unburned areas, which may result in better survival and offset the lower numbers of germinants observed in burned versus unburned areas on the ESSF intensive site.

The apparent lack of species requiring fire to germinate (with the possible exception of *Paxistima myrsinites*) is consistent with the relatively low frequency of natural fire in the study area. In fact, the seeds of several taxa appeared to be destroyed by fire (*e.g. Mitella* spp., *Vaccinium* spp.).

The distribution of most germinant species both within and among sites was inconsistent. Within-site variation was probably due to the clustered distribution of buried seeds, and variations in microtopography and fire severity. Differences in site productivity, burn severity and vegetation history were probably responsible for between-site variation.

Of the two germinant species found on all sites, one likely did not originate from the seed bank. Most germinant taxa found on the intensive sites were also found in some extensive sites, and were generally not confined to particular variants or ecosystems.

A large proportion of buried seeds were likely consumed during fire because of their concentration in the top 3 cm of the forest floor. Only a small fraction of seeds remaining in the unconsumed forest floor germinated, possibly because: 1) seeds were also killed by elevated temperatures during the fire or 2) post-burn conditions were unfavourable to germination.

The study could not distinguish between these two possibilities because the temperatures seeds were exposed to during the burn could not be determined and the heat tolerances of seed bank species found in this study are unknown. A larger sample size and the inclusion of other important factors, such as soil moisture and texture, would be required to construct a model of soil heating.

There appeared to be a threshold depth of burn beyond which no germination occurred on both sites. This suggests that temperatures reached during the fire were lethal to seeds in the remaining forest floor. The length of exposure to elevated

temperatures in this study has been shown to kill seeds of some species.

In the post-burn environment, burning appears to have affected germination more than did shading, while shading appeared to have had a greater influence on soil temperatures than did burning. These results suggest that forest floor temperature was not of primary importance to germination. However, without 1) replication of temperature measurements, 2) measurement of temperatures where germination was being monitored, and 3) information on the effect of different temperature regimes on germination of the seed bank species found in this study, little can be concluded about the importance of temperature regime to germination or about the factors affecting temperature regime.

4.2 **Recommendations**

The species composition, numbers and distribution of buried seeds should be further investigated in B.C. forest soils, especially in moister, richer ecosystems. Studies should be replicated within ecosystems to determine between-site variation. This information would extend current knowledge of the geographical and ecological distribution of seed bank species.

Research is needed on the importance of seed banks to revegetation after fire and other disturbances. Determining the relative contribution of seed banks and other sources of plants (*e.g.* bud banks, seed rain and seedling banks) to post-disturbance vegetation would require long-term monitoring of individual plants of different origins. The effect of different

types and severities of disturbance on the mode of revegetation of individual species and plant communities, would be a useful basis for planning forest management activities.

Research on seed banks should focus specifically on 1) measuring factors in the environment that could influence buried seeds (*e.g.* soil moisture, temperature, light and chemistry), 2) measuring changes in the seed environment during and after disturbance, and 3) determining, through controlled experiments, how seeds respond to such changes. Experiments on seed bank species should determine: 1) the depth from which seeds can germinate, 2) the magnitude and duration of temperature exposure that is lethal, and 3) the optimal temperature, moisture and chemical environment for post-disturbance seed germination.

In order to maintain the contribution that seed banks make to the natural diversity of forest ecosystems, research is also needed to determine : 1) the longevity of buried seeds in forest soils, 2) the relationship between source plant abundance and buried seed abundance, 3) the relationship between forest structure and production of seed in forest understory species, 4) the means by which seeds become buried, and 5) the relationship between the distribution of seeds, the distribution of plants, and mode of seed dispersal.

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