

**The effects of site and soil properties on
the establishment and early development
of *Pinus sylvestris* and *Picea abies*
regenerated from seeds**

Michelle de Chantal

Academic dissertation

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Abstract

de Chantal, M. 2003. The effects of site and soil properties on the establishment and early development of *Pinus sylvestris* and *Picea abies* regenerated from seeds. University of Helsinki Department of Forest Ecology Publications 27.

The establishment and early development of seedlings of the two native conifer species in Finland, shade-intolerant *Pinus sylvestris* L. (Scots pine) and shade-tolerant *Picea abies* (L.) Karst. (Norway spruce), were studied in relation to site and soil properties. This topic is of great concern because seedling growth patterns and morphological characteristics play an important role in determining competitive ability for establishment, promoting increased growth, and influencing succession dynamics after a disturbance.

Sowing date proved to be an important factor to consider when regenerating forests from seeds. Seedlings from spring sowings were larger than those from summer sowings. In addition, summer-sown seedlings were more susceptible to frost heaving than spring-sown seedlings, and were exposed at early stages to dry and warm environmental conditions, which can cause drought. Accordingly, it is advisable to sow seeds as early as possible in spring when regenerating forests through direct seeding. However, the strong effect of sowing date on seedling size may be a consequence of frost heaving injuries, which may have injured roots and limited seedling growth.

Site preparation methods that expose the E/B horizon should be used when regenerating sites using direct seeding or natural regeneration, especially on moist, fine-textured soil. Mounding and site preparation methods that expose the C horizon should be avoided, as these treatments had negative effects on soil water conditions that resulted in increased mortality when the growing season was dry. Because volumetric soil water content of exposed C horizon was always low, independently of growing season climate, exposed C horizon should be used with caution, especially when regenerating sites with single-grained coarse-textured soil. In addition, seedlings growing on exposed C horizon were smallest. Furthermore, seedlings growing on mounds and exposed C horizon were prone to frost heaving, which was detrimental to seedling establishment, especially on moist, fine-textured soil. Nevertheless, from the point of view of seedling growth, mounds were the most favourable site for the regeneration of *P. sylvestris* through direct seeding. Considering the above-mentioned factors and risks, exposed E/B horizon is a good alternative when regenerating *P. sylvestris* forests through direct seeding or natural regeneration.

The results showed that although site preparation, and consequently soil texture and structure, had a strong effect on volumetric soil water content and water retention capacity, they had only a minor effect on seedling emergence when environmental conditions were moist. When soil water and relative humidity were high, precipitation and capillary water movement kept the soil surface moist enough for seed germination. However, dry and warm weather had a negative impact on seedling emergence.

Emergence and establishment of *P. sylvestris* seedlings were improved with exposed C and E/B horizons on stabilised soil, though no significant differences in soil properties were observed between fresh and stabilised site preparation treatments. Thus, *P. sylvestris* could benefit from soil stabilisation, except when regenerating using mounds. However, it is not advantageous to wait for soil to stabilise before

regenerating *P. abies* from seeds. Mortality due to frost heaving did not differ significantly between freshly prepared and stabilised soil.

During early development, shade-intolerant *P. sylvestris* underwent morphological modifications that allowed it to capture more light and compete better for resources than shade-tolerant *P. abies* in gap-edge environments. Aboveground dry biomass, height, and projected leaf area of both species increased with increasing radiation, but *P. sylvestris* responded more strongly than *P. abies*. In addition, *P. sylvestris* responded to radiation with a more flexible needle length than *P. abies*. With increasing radiation, *P. sylvestris* seedlings allocated proportionally more aboveground dry biomass to assimilating parts versus structural parts compared to *P. abies*. However, the lack of convergence between the spatial distributions of seedling size variables and radiation indicates that seedlings growing in the gap-edge zone were also affected by environmental factors other than radiation, e.g. root competition for water and nutrients by ground vegetation and mature trees. Judging from the asymmetric distributions of radiation and seedling size responses in relation to the circular gap, seedlings would benefit optimally from radiation if gaps had an elongated shape and a north-south orientation. This shape and orientation of gaps would maximise the area receiving the most radiation in the central part of the gap, while simultaneously minimising the area receiving the least radiation at the southern edge of the gap.

Key words: emergence, frost heaving, gap-edge zone, moisture, morphology, mortality, nutrients, radiation, soil stabilisation, soil texture, sowing date

List of original articles

This doctoral thesis comprises the following original articles, which are referred to in the text according to their Roman numerals:

- I. Michelle de Chantal, Kari Leinonen, Hannu Ilvesniemi, and Carl Johan Westman. 2003. Combined effects of site preparation, soil properties, and sowing date on the establishment of *Pinus sylvestris* and *Picea abies* from seeds. In press, Can. J. For. Res. (Reprinted with kind permission of NRC Research Press.)
- II. Michelle de Chantal, Laura Eskola, Hannu Ilvesniemi, Kari Leinonen, and Carl Johan Westman. 2003. Early establishment of *Pinus sylvestris* and *Picea abies* sown on soil prepared freshly and after stabilisation. *Silva Fennica*, 37 (1): 15-30. (Reprinted with kind permission of the Finnish Society of Forest Science and the Finnish Forest Research Institute.)
- III. Michelle de Chantal, Kari Leinonen, Hannu Ilvesniemi, and Carl Johan Westman. 2003. Effects of soil preparation on soil properties and on morphology of *Pinus sylvestris* and *Picea abies* seedlings sown at different dates. In press, *New Forests*. (Reprinted with kind permission of Kluwer Academic Publishers.)
- IV. Michelle de Chantal, Kari Leinonen, Timo Kuuluvainen, and Alessandro Cescatti. 2003. Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest. *Forest Ecology and Management*, 176 (1-3): 321-336. (Reprinted with kind permission of Elsevier.)

Michelle de Chantal participated in planning the research, was responsible for data collection, data analysis, and literature searches, and was the main writer in all Studies; she was also responsible for setting up the experiment in Studies I-III. Kari Leinonen participated in planning the research, advised on experimental design and statistical methods, participated in discussions, and commented on the manuscripts in all Studies; he also participated in setting up the experiment in Study IV. Hannu Ilvesniemi participated in planning the research, advised on soil analyses, participated in discussions, and commented on the manuscripts in Studies I-III. Carl Johan Westman participated in planning the research, advised on soil analyses, participated in discussions and in the writing of the soil results, and commented on the manuscripts of Studies I-III. Timo Kuuluvainen participated in planning the research and setting up the experiment, advised on statistical methods and seedling measurements, participated in discussions and in the writing of the manuscript in Study IV. Alessandro Cescatti was responsible for the radiation modelling, participated in discussions and in the writing of the "Radiation modelling" section, and commented on the manuscript in Study IV. Laura Eskola participated in data collection and used part of the data of Study II for her Master's thesis, which was used as the first draft for the article.

Equivalencies

List of equivalencies between FAO and Canadian Soil Taxonomy systems. The FAO system is used throughout the thesis summary and Studies II and III. The Canadian system is used in Study I.

FAO	Canadian	Description
H	O	Organic horizon composed of mosses and woody material
O	L-F, L-H, F-H	Forest litter at various stages of decomposition
E	Ae	Mineral horizon characterized by the eluviation of clay, Fe, Al, and/or organic matter
B	B	Mineral horizon enriched in organic matter, clay, and/or sesquioxides
Bs	Bf	Mineral horizon enriched with Al and Fe combined with organic matter; contains 0.5-5% organic C
C	C	Coarse-textured mineral horizon

The terms “block” (summary, Studies I and II) and “gradient position” (Study III) refer to the same classification factor used to describe the spatial variation in soil properties, such as particle size, water retention, water content, nutrients, and temperature, along the slope. Alternatively, “slope” is used when reporting results in a general way.

1. Introduction

In Finland, silvicultural methods such as natural regeneration with shelterwood systems and seed trees, forest management methods using small-scale natural disturbances as a template, and direct seeding have become more popular with the decrease of large-scale planted clearcuts. Nowadays, half of forest cuttings are regenerated from seeds: 20% using direct seeding and 30% through natural regeneration (Finnish Statistical Yearbook of Forestry 2001). The Finnish Forest Act requires a forest site to be adequately regenerated as soon as possible after tree harvest (Ministry of Agriculture and Forestry 1997). Accordingly, site preparation is commonly used in combination with direct seeding or natural regeneration to promote prompt forest tree regeneration by creating more favourable microsites for seedling emergence, establishment, and growth (Örlander et al. 1990; Prévost 1992; Sutton 1993). Site preparation treatments such as mounding, scarification, harrowing, and ploughing, are presently applied to 58% of forest regeneration areas (Finnish Statistical Yearbook of Forestry 2001). Likewise, forests with canopy gaps are a common part of the landscape in Finland, as the average size of clearcuts is 1-4 ha.

Although the establishment and early development of the native conifer species of Finland, i.e. *Pinus sylvestris* L. (Scots pine) and *Picea abies* (L.) Karst. (Norway spruce), have been studied for several decades (e.g. Yli-Vakkuri 1961b), no studies have addressed the subject in comprehensive details. This topic is important because seedling growth patterns and morphological characteristics play an important role in determining competitive ability for establishment, promoting increased growth, and influencing succession dynamics after a disturbance (Goulet and Bellefleur 1986; Zobel and Antos 1991; Tremmel and Bazzaz 1995). Even small differences in morphology and growth may be ecologically important for survival (Walters and Reich 1996), especially on sites where competition from ground vegetation is strong (Nilsson et al. 1996; Örlander et al. 1996; Jäderlund et al. 1997; Nilsson and Örlander 1999). With particular stress on the risk arising from competing vegetation, today's forestry practices in Finland strive to sow seeds in conjunction with the site preparation treatment, or to plan the site preparation so that it corresponds with the period of natural seed rain. In order to improve the success of existing direct seeding and natural regeneration methods, and to develop new ones, more detailed information about the effects of soil properties, site preparation, sowing date, and canopy gaps on forest regeneration from seeds is required.

2. Aims

In this thesis, I studied the regeneration of shade-intolerant *P. sylvestris* and shade-tolerant *P. abies* seedlings. I was interested to know the effects of site conditions, such as site preparation, soil properties, and small canopy gaps, on seedling establishment and early development. For this purpose, I undertook four studies dealing with specific aspects of seedling regeneration. Three experiments took place in a clearcut on a slope with variation in soil water, texture, and fertility (Studies I-III), and one experiment was conducted in a small canopy gap (Study IV).

It was hypothesised that exposed E/B horizon would retain more soil water than mounds or exposed C horizon, and that soil properties would affect seedling regeneration (Studies I-III). In addition, I wanted to know how changes in radiation due to a small canopy gap would affect the early development pattern of shade-intolerant *P. sylvestris* and shade-tolerant *P. abies* (Study IV).

To achieve these goals, I examined the effects of site preparation, soil properties, and sowing date on the emergence, mortality, and early establishment of *P. sylvestris* and *P. abies* seedlings (Study I). In addition, I compared the emergence, mortality, and early establishment of *P. sylvestris* and *P. abies* seedlings on soils freshly prepared and soils left to stabilise for one year after site preparation (Study II). Furthermore, I investigated the effects of site preparation on soil properties and on the morphology of three-year-old *P. sylvestris* and *P. abies* seedlings sown at different dates (Study III). I also determined the early response of size and morphology of two-year-old *P. sylvestris* and *P. abies* seedlings to a gap-edge zone (Study IV). Finally, I studied the effect of moist chilling of seeds on seedling size and morphological development (Study IV).

3. Factors affecting seedling regeneration

Seedling regeneration encompasses seedling emergence and establishment, as well as early development. The first factors affecting regeneration are seed germination and seedling emergence. Seed germination, defined as radicle protrusion from the seed coat, is a phenomenon that is not easily observed in the field, especially if the seed is partly buried in soil. In contrast, seedling emergence, or the appearance of a stem above the soil, is more easily observed, and is the concept used in this thesis. The survival of emerged seedlings is directly affected by various factors, such as predation, drought, and frost heaving. In addition, seedling survival is indirectly affected by soil properties, e.g. moisture and texture. Because the number of living seedlings decreases with time, seedling survival and mortality influence the resulting seedling establishment, which is defined as the proportion of living seedlings at a specific time point in relation to the number of sown seeds. In turn, the morphological development of established seedlings is influenced by site conditions.

Site conditions can be modified using site preparation and small canopy openings. Site preparation modifies soil structure, and changes nutrient and water availability, as well as soil temperature (Örlander et al. 1990; Prévost 1992; Sutton 1993), which in turn affect seedling establishment and development. Moreover, soil properties can change with time due to soil stabilisation after site preparation. Similarly, canopy gaps modify environmental conditions in the gap-edge zone, such as radiation, microclimate, soil water, and nutrient availability (Matlack 1993; Chen et al. 1995; Palik et al. 1997), and thus influence seedling establishment and development. Factors that affect regeneration success and that are studied in this thesis, either directly or indirectly, are illustrated in Figure 1.

3.1. Soil properties

Soil moisture, temperature, evaporation, and relative humidity (RH) are important factors affecting seed germination and seedling emergence (Winsa 1995; Oleskog and Sahlén 2000; Oleskog et al. 2000). Thus, low or high temperatures and low soil water can delay or prevent seedling emergence (Bergsten 1989; Leinonen et al. 1993; Oleskog and Sahlén 2000). Delays in seedling emergence increase the risk of losses due to seed desiccation and predation (Vaartaja 1954; Jinks and Jones 1996; Smith et al. 1997). Furthermore, periods of low soil water availability increase seedling mortality, especially in combination with high soil temperature and the consequently high evaporation (Thomas and Wein 1985; Fleming et al. 1994; Haeussler et al. 1995).

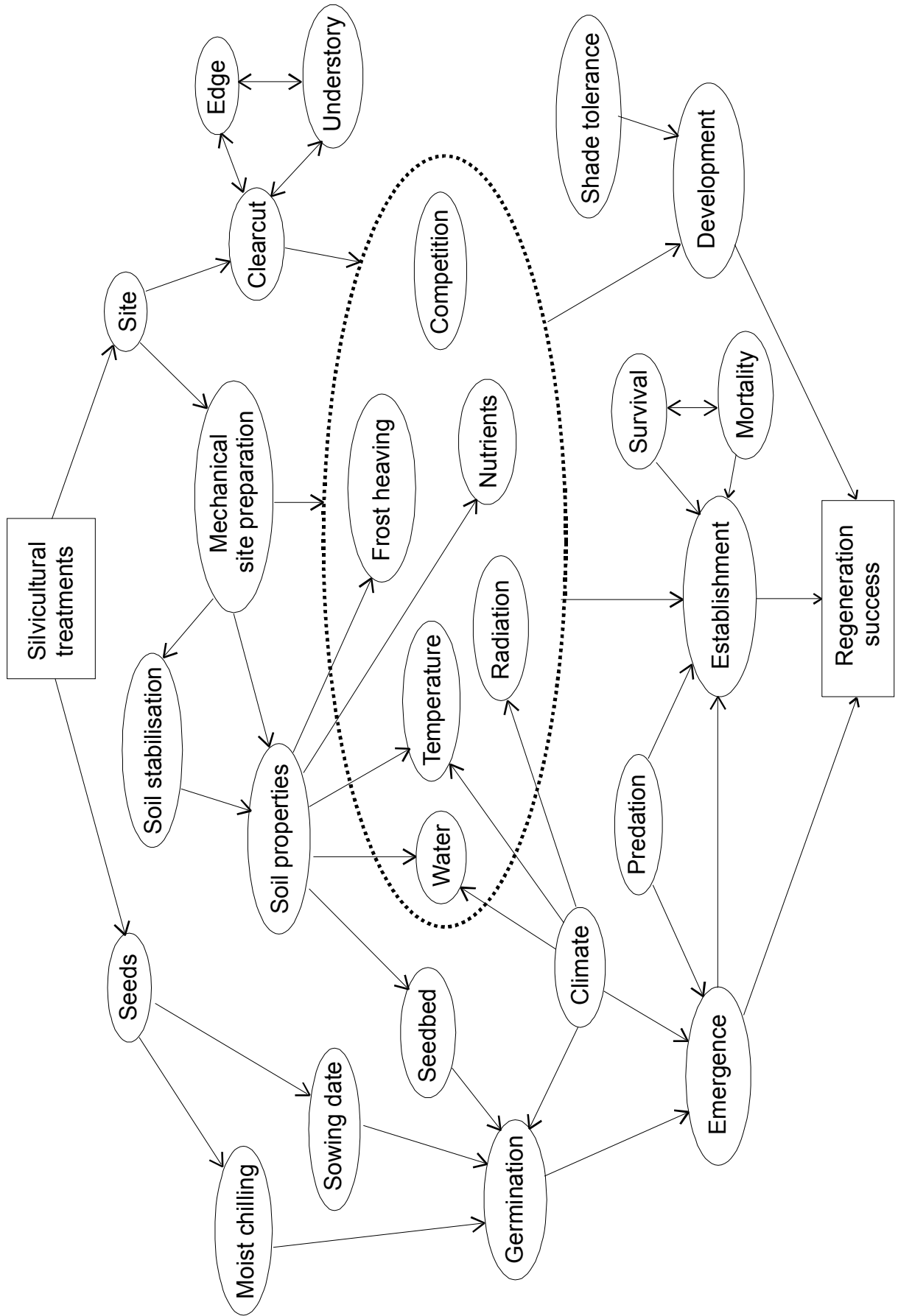


Figure 1. Diagrammatic illustration of factors affecting regeneration success.

The availability of soil water for seedling emergence, establishment, and growth depends on the texture and structure of the soil. Water drains quickly from coarse-textured soils. In contrast, a high content of fine soil particles (e.g. < 0.06 mm in diameter) and organic matter in soil favour water retention (Mecke and Ilvesniemi 1999; Mecke et al. 2000). In that respect, the accumulation of organic compounds and sesquioxides between mineral particles in the B horizon change pore size distribution to smaller pores, thus increasing water-holding capacity (Mecke et al. 2002). However, soils that retain more water are also more susceptible to frost heaving (Goulet 1995), which can cause seedling mortality. Seedling survival is greater once roots have reached a depth at which water supply is more stable, i.e. where water evaporation is less important.

Soil texture also affects soil nutrient availability and primary site productivity. Consequently, the amount of C and N in soil is correlated to the content of particles <0.02 mm, i.e. silt and clay (Hassink 1997). However, several studies have demonstrated that bacterial decomposition of organic matter, which is necessary for N mineralisation, takes place faster in coarse-textured than in fine-textured soil (Van Veen and Van Elsas 1986). This is because organic matter present in fine-textured soil is partly unavailable for bacterial decomposition, either through adsorption onto clay particles or entrapment within small pores non-accessible to the soil micro-fauna (Van Veen and Van Elsas 1986; Van Veen and Kuikman 1990; Strong et al. 1999). In addition, soil aeration conditions are more favourable for micro-organism activity in coarse-textured than in fine-textured soils.

With site preparation, soil texture and structure may be modified such that pore size is increased, and organic matter becomes exposed, thus becoming available to bacterial decomposition and mineralisation. The increased soil temperature of prepared soil compared to undisturbed ground (Kubin and Kemppainen 1994; Fleming et al. 1998) can affect the availability of soil nutrients positively, as decomposition of organic matter is increased by warm soil temperatures and by mixing with mineral soil (Salonius 1983). Site preparation also modifies aeration by decreasing bulk density (Ritari and Lähde 1978).

These changes in soil properties can have both beneficial or detrimental effects on seedling morphology which can be observed for several years after site preparation (Sutton 1991; Prévost 1992; Sutton 1993). For example, high nutrient and moisture availability, as well as warmer soil temperatures benefit shoot and root biomass growth (Örlander et al. 1990; Sutton 1991), whereas high soil bulk density can reduce height growth and root elongation (Prévost and Bolghari 1990; Prévost 1992). In addition, high N promotes branch production and modifies biomass allocation patterns in seedlings (Knight 1973; Will 1977). In contrast, in conditions of low soil water and nutrient availability, seedlings will allocate proportionally more biomass to roots (Timmer and Armstrong 1989; Brand 1991; Sutton 1991; Timmer and Miller 1991; Ericsson 1995). Therefore, it is of interest to know how site preparation affects soil properties, and in turn, seedling emergence, establishment, and morphology of seedling regenerated from seeds.

3.2. Sowing date

Weather affects soil temperature and moisture, and consequently, sowing date is an important factor affecting seedling emergence and establishment. Seeds sown earlier in the spring have higher rates of seedling emergence and survival than seeds from later sowings (Kinnunen 1992; Jinks and Jones 1996). Warmer soil temperatures

occurring later in the summer, and the consequently lower soil water and higher evaporation, can reduce emergence rates through seed desiccation, and can kill seedlings through drought (Jinks and Jones 1996; Smith et al. 1997). Sowing date influences seedling growth as spring-sown seedlings can benefit from a longer growing season than summer-sown seedlings (Mexal and Fisher 1987; Boyer and South 1988; Kinnunen 1992; Jinks and Jones 1996; Wang and Lechowicz 1998; Winsa and Sahlén 2001). With few exceptions (Mexal and Fisher 1987; Wang and Lechowicz 1998), studies on the effect of sowing date on seedling morphology have dealt mainly with height and diameter growth. Therefore, it is important to know if sowing date has a prolonged effect on other morphological characteristics.

In addition, seed treatments may be applied to modify the properties of collected boreal tree seeds used in direct seeding. For this purpose, moist chilling can be used to relieve seed dormancy and to widen the environmental range for germination (Gosling and Peace 1990; Leinonen and Rita 1995; Leinonen 1997), thus promoting fast and high seedling emergence. Accordingly, moist chilling impacts on timing of germination, and on the length of the first growing season.

3.3. Soil stabilisation

Freshly prepared soil is susceptible to frost heaving, especially after wet summers, which increases seedling mortality. In order to diminish the risk of losses due to frost heaving, site preparation should be allowed to stabilise for up to two years before sowing seeds (Pohtila 1977). However, a long time period between site preparation and sowing can be detrimental to regeneration success (Pohtila and Pohjola 1985; Solbraa and Andersen 1997) as seedbed receptivity diminishes with time after site preparation (Arlidge 1967; Fleming and Mossa 1995; Karlsson and Örlander 2000). Vegetation may gradually overtake the sowing areas, thus decreasing seedbed receptivity and competing with seedling establishment (Arlidge 1967; Örlander et al. 1990; Fleming and Mossa 1995; Nilsson et al. 1996; Nilsson and Örlander 1999). Litter accumulation may also reduce the area of receptive seedbed (Fleming and Mossa 1995). In addition, the receptivity of seedbeds depends on yearly climate and soil water content (Fleming and Mossa 1995).

During the soil stabilisation period, the beating action of raindrops on exposed soil breaks up soil aggregates, such that percolation water causes fine soil particles to move into macropores, thus sealing pores and forming a surface crust. In addition, settling of soil occurs due to wetting-drying and freeze-thaw cycles, which make the soil shrink and swell in alternance, thus promoting the compaction of soil aggregates (Kozłowski 1999). On mounds, the compaction is further enhanced by the weight of snow (Heineman 1999). As a consequence of soil settling and compaction, soil pore size distribution changes, such that the fraction of small pores increases (Kozłowski 1999). After the formation of a surface crust, and following soil settling and compaction, air-filled porosity and water infiltration decrease, whereas bulk density increases (Kauppila and Lähde 1975; Hillel 1980; Kozłowski 1999). However, mild compaction may be beneficial as it improves capillary movement of soil water (Kozłowski 1999).

Fertility of mounds containing humus mixed with mineral soil increases with time elapsed since site preparation as conditions for bacterial decomposition of organic matter are improved (Salonius 1983). Consequently, nutrient availability to seedlings is increased.

3.4. Gap-edge zone

Small-scale gap disturbance and regeneration are an integral part of the dynamics of boreal forests (Bergeron et al. 1999; Engelmark and Hytteborn 1999). In naturally dynamic boreal forests of Fennoscandia, small gaps are commonly created by minor perturbations, such as surface fire, strong winds, pathogens, or heavy snow loads (Sernander 1936; Liu and Hytteborn 1991; Kuuluvainen 1994). Accordingly, forest management methods that simulate natural disturbances are being developed (Attiwill 1994; Bergeron and Harvey 1997; Angelstam 1998; Franklin et al. 2002; Harvey et al. 2002; Kuuluvainen 2002). As a result, forest gaps are also man-made through forest harvesting using silvicultural methods that include the use of small and/or irregularly shaped clearcuts that are broken with islands of retention trees (Coates and Burton 1997). With the promoted use of small-scale silvicultural methods, more regeneration area is in a gap-edge environment (Matlack and Litvaitis 1999).

Gap environments are heterogeneous with fine-scale environmental variation in regeneration microhabitats (Kuuluvainen and Juntunen 1998) superimposed by large-scale within-gap gradients in competitive interference for light, water, and nutrients by the dominant trees surrounding a gap (Aaltonen 1919; Goldberg 1990; Kuuluvainen et al. 1993; Palik et al. 1997). Surrounding trees also have a strong effect on the environmental conditions and processes in the gap area, especially in the vicinity of gap edges (Chen et al. 1993; Matlack 1993; Chen et al. 1995; Cadenasso et al. 1997; Matlack and Litvaitis 1999). These effects modify the distribution of resources along the gap-edge zone, which can lead to gap partitioning.

4. Material and methods

4.1. Study sites

For Studies I-III, the experiments were established in a 2 ha clearcut near the Hyytiälä Forestry Field Station of the University of Helsinki, Finland (61°48'N, 24°19'E, 151-153 m a.s.l.). The site is on a gentle slope (3.4%) with variation in soil water and texture from a dry coarse-textured *Vaccinium vitis-idaea* forest site type (VT; Cajander 1925) formerly dominated by *Pinus sylvestris* on the upper slope, to intermediate *Vaccinium myrtillus* forest site type (MT) formerly covered by a mixed *P. sylvestris* and *P. abies* forest at mid-slope, to a mesic, more fertile, fine-textured *Oxalis acetosella-Vaccinium myrtillus* forest site type (OMT) formerly dominated by *P. abies* on the lower slope. *Betula pendula* Roth (silver birch) was also present in small numbers. *Pinus sylvestris* is a shade-intolerant species that grows naturally on dry sandy soils, whereas *P. abies* is a shade-tolerant species that prefers moist, fertile or medium fertile sites. The forest was harvested by machine in winter, and logs were removed from the site at the same time, so the snow cover protected the soil against any disturbance. Before clearcutting, timber productivity followed the fertility gradient, with aboveground tree biomasses of 13.7, 15.1 and 16.3 kg m⁻², respectively, for the VT, MT, and OMT sites. Mecke and Ilvesniemi (1999) described the hydrological properties of the site before harvest. The parent soil is a glaciofluvial deposit. Total annual precipitation in the region of the experimental site was 825 mm in 1998, 676 mm in 1999, and 481 mm in 2000 (Hyytiälä Forestry Field Station meteorology data). Average precipitation and air temperature (AT) during the growing season in the region of the experimental site were 496 mm and 12.6°C in 1998, and

234 mm and 14.0°C in 1999, respectively (Hyytiälä Forestry Field Station meteorology data).

The experimental work for Study IV was set in an even-aged 80-year-old coniferous stand (2 ha) located 6.5 km from the Hyytiälä Forestry Field Station. The dominant species in the stand is *P. abies*, which accounts for 94% of the stems, while *P. sylvestris* and *B. pendula* each represent 3% of the stems. In order to create a gap-edge zone, trees were removed in winter 1995 from a circular gap about 50 m in diameter (2200 m²) in the centre of the stand. Before cutting, the growing stock density was 462 stems/ha, volume 256 m³/ha, and the average height 20.2 m. The stand is located on a glacial delta formation of fine sand (particle size 0.2-0.02 mm) and the soil type is podzolic. According to the Finnish classification of forest types, the site is a *Myrtillus* site type (MT). The understorey vegetation consisted of mosses during growing season 1995, and light *Deschampsia* spp. and *Calamagrostis* spp. growth during growing season 1996.

The 1961-1990 average for annual precipitation in the region of the study sites is 709 mm, and mean annual temperature is 2.9°C (Finnish Meteorological Institute 1991). Average precipitation during the growing season (May-September) in the region is 361 mm and mean AT is 13.2°C (Finnish Meteorological Institute 1991).

4.2. Site preparation treatments

Three types of site preparation treatments were studied: exposed C horizon, exposed E/B horizon, and mounds. For exposed C horizon, the humus layer (O horizon) and mineral soil were removed down to the surface of C horizon at 20-25 cm depth. Because of its coarse soil texture, exposed C horizon is expected to have low water retention capacity. In addition, fertility should be low because very little organic matter is found at 20-25 cm depth in soil.

The humus and mineral soil removed in order to expose the C horizon were roughly mixed and piled up over undisturbed ground to form mounds, 20-25 cm high (broken O/E/B horizons). The humus buried inside the mounds should provide increased fertility (Salonius 1983). However, the broken soil structure may have a decreased water retention capacity.

Exposed E/B horizon was made by removing the O horizon to expose the mineral soil surface. Due to its intact soil structure and fine soil texture, exposed E/B horizon is expected to have high water retention capacity. In addition, soil fertility should be high due to leaching from the E horizon into the B horizon.

4.3. Experimental designs

In order to study the effect of site preparation, soil properties, soil stabilisation, and sowing date on the establishment and early development of *P. sylvestris* and *P. abies* seedlings (Studies I-III), parallel experiments of similar split-plot design were established in the clearcut in 1998 and 1999. In the spring of both years, eight blocks of 10 × 15 m were delimited perpendicular to the slope (Fig. 1a in Study I) and cleared from woody debris larger than a few centimetres in diameter. Blocks were laid out along the slope to cover the variation in soil properties, such as particle size, water retention, volumetric soil water content, and temperature. Block 1 is located on the drier upper slope, and block 8 on the moister lower slope.

Separate split-plot designs (though over the same area) were used for *P. sylvestris* and *P. abies*. The main plot units consisted of three site preparation treatments (exposed C horizon, mounds, and exposed E/B horizon; Fig. 1b in Study I) randomised and replicated three times within each block. Site preparation plots were

roughly made using an excavator, and finition was done using a shovel to make sure the soil horizons were as intact as possible. Site preparation plots were about 1 m² each, and were spread out uniformly between stumps over a total area of 1200 m², i.e. about 1-2 m from each other.

Each site preparation plot was subdivided into subplots where two sowing dates, spring (May) and summer (June), were randomised. A sowing area of 22 × 18 cm was marked on roughly levelled soil in the centre of each site preparation subplot. Each sowing area contained 20 sowing microsites of equal size (4.4 × 4.5 cm), in a 5 × 4 grid pattern. One seed was sown uncovered in a 2-mm deep depression at the centre of each of these microsites, in spring and summer 1998 and 1999, in order to examine the effects of site preparation, soil properties, and sowing date on seedling establishment (Study I).

To examine the effect of soil stabilisation on seedling establishment (Study II), seeds were sown in spring 1998 on fresh site preparation, and in spring 1999 both on fresh site preparation, and on site preparation that was done in 1998 and left to stabilise for one year, following the same procedure as in Study I.

To study the effects of site preparation, soil properties, and sowing date on seedling morphology (Study III), the surviving three-year-old *P. sylvestris* and *P. abies* seedlings from the spring and summer sowings of 1998 were randomly sampled in autumn 2000 from each site preparation plot, in every block and for each sowing date (see Study III for details).

The effects of a gap-edge zone and moist chilling on the size and morphological development of *P. sylvestris* and *P. abies* seedlings were examined in Study IV. In order to get a radiation gradient from the centre of the gap to all directions, an experimental area of 72 × 72 m was placed over the gap and its edges, and divided into 64 blocks of equal size (9 × 9 m), in an 8 × 8 grid pattern (Fig. 1a in Study IV). Block represents spatial location and includes the variation in radiation, soil properties, water availability, competition, and other variables along the gap-edge zone. In each block, four plots of 40 × 40 cm in area, and a few centimetres deep into the humus, were scalped to the mineral soil (Fig. 1b in Study IV). In the centre of each of these 256 plots, a sowing area of 22 × 18 cm was marked and subdivided into 20 sowing spaces of equal size, in a 5 × 4 grid pattern (Fig. 1c in Study IV). Each sowing space received one seed in June 1995. A 2 × 2 factorial design (species × moist chilling) was used, allocated randomly between plots in each block, each plot containing twenty seeds of the same species and treatment. Moist chilling was used in order to reproduce the natural conditions occurring in boreal forests (Heikinheimo 1937). It was induced by storing *P. sylvestris* and *P. abies* seeds (from the same seed source as unchilled seeds) at 3 ± 1°C on moist filter paper under cool white light (16 h photoperiod; 25–30 μmol·m⁻²·s⁻¹) during 4 weeks. The surviving two-year-old *P. sylvestris* and *P. abies* seedlings were randomly sampled for size and morphology measurements in October 1996 (see Study IV for details).

4.4. Seedling measurements

Seedling emergence, mortality (reduction in living seedlings between two time points), and establishment were inventoried regularly during the growing seasons (Studies I and II). Inventories were made every second day during the first month after sowing, weekly at the end of the first growing season, and monthly during subsequent growing seasons. Specific causes of mortality were not identified, except

frost heaving. Frost heaved seedlings were clearly identifiable as their roots had been totally or partially expelled from the soil.

To evaluate the effect of site preparation and sowing date on seedling morphological characteristics, a sample of seedlings was measured (Study III). The characteristics measured were shoot and root dry biomass, height, total branch length, root length, and root surface area (see Study III for measurement details). In addition, seedling morphological characteristics were described using the following ratios: height/shoot dry biomass (seedling slenderness), shoot/root dry biomass, specific root length (root length/root dry biomass), and specific root surface area (root surface area/root dry biomass).

Foliar N concentration of spring-sown *P. sylvestris* seedlings was compared between site preparation treatments using vector analysis (Haase and Rose 1995). For this purpose, a combined sample of dry milled needles was obtained from three-year-old *P. sylvestris* seedlings growing on each site preparation plot (see Study III for details).

In order to evaluate the effect of the gap-edge zone and moist chilling on aboveground seedling size and morphology (Study IV), total needle dry biomass, stem dry biomass, projected leaf area, mean needle length, and height were measured on a sample of seedlings. In addition to the dimensional variables measured directly on seedlings, some indices expressing seedling morphology were calculated. In order to determine whether *P. sylvestris* and *P. abies* allocate resources differently between photosynthesising and structural parts along the gap-edge zone, the distribution of dry biomass between needle and stem was calculated. Specific leaf area_p (projected leaf area/total needle dry biomass) is an indirect evaluation of relative growth rate (Reich et al. 1998; Wright and Westoby 2001), and was measured to determine differences in growth strategies between species. Aboveground seedling morphology shows how seedlings compete for space and light, and is evaluated on the basis of height/stem dry biomass and mean needle length.

4.5. Soil measurements

Soil properties were measured (see Studies I-III for details) in order to relate seedling emergence, mortality, and establishment, as well as morphological characteristics to the growth conditions created by the different site preparation treatments.

From each site preparation plot, soil water content at 5 cm-depth was monitored weekly during all growing seasons using TDR probes (Heimovaara 1993). Soil temperature at 5 cm-depth was recorded at 10-minute intervals throughout the years using copper-constantan temperature sensors installed in 9 replicates (6 installed in 1998 and 3 in 1999) from each site preparation treatment, located on the upper, mid-, and lower slope. Near saturated soil hydraulic conductivity at -11 cm pressure head (K_{11}) was measured in the field during summer 1999.

In the laboratory, soil moisture desorption curves, soil particle size distribution, loss-on-ignition (LOI), bulk density, and organic carbon content were measured from soil cores. Water retention capacity at -10 kPa matric suction (field capacity) and -50 kPa, the recommended irrigation limits for nursery tree seedlings (McDonald 1984), as well as air-filled porosity at -10 kPa (water retention at saturation minus water retention at -10 kPa) were calculated from the soil moisture desorption curves.

4.6. Radiation modelling

Radiation penetrating through canopy gaps influences other variables, such as soil and air temperature, soil water and nutrient availability. For this reason, radiation was chosen to characterise the gap-edge zone. Because empirical measurements of radiation over the growing season in numerous locations (256) would have been very tedious, a modelling approach was adopted to describe the radiation regime. For this task, radiation values at each seedling location were predicted by a radiative transfer model specially calibrated and evaluated for the study stand (see Study IV for details). A complete description of the model theory and application to the specific study area is reported in Cescatti (1997a, b).

4.7. Statistical analyses

For all studies, data were analysed using analysis of variance (see Studies I-IV for complete models). All analyses of variance were calculated using the GLM procedure of SAS (SAS Institute Inc. 1989).

In Study I, the effects of block, site preparation, and sowing date on volumetric soil water content were tested separately for each growing season. In addition, for each species and sowing year, the effects of block, site preparation, and sowing date on seedling emergence, mortality, and establishment were tested using an ANOVA model for a split-plot design. The emergence, mortality, and establishment percentages were arcsin-transformed (using radians) for the analysis because the variance is a function of the mean in a binomial distribution (Zar 1999, p. 278-280). Differences between site preparation treatments were evaluated using Student-Newman-Keuls (SNK) multiple range test (Zar 1999, p. 214-215).

In Study II, soil properties, seedling emergence, mortality, and establishment were compared in two ways (Fig. 3 in Study II). First, the same site preparation plots were compared as freshly prepared and after the soil had stabilised for one year. The differences in climate between years is a confounding factor in this comparison. Second, different fresh and stabilised site preparation plots were compared during the same time period. In this case, the climate was the same, but the original soil properties were different. The effects of block, soil stabilisation, and site preparation on soil properties were tested using a model for a split-plot design. In addition, the effects of block, soil stabilisation, site preparation, and species on emergence, mortality, and establishment of *P. sylvestris* and *P. abies* seedlings were tested using a model for a split-plot design. Similarly as in Study I, the emergence, mortality, and establishment percentages were arcsin-transformed (using radians) for the analyses. In addition, hydraulic conductivity was log-transformed (base-e log) for the ANOVA. Differences between site preparation or soil stabilisation treatments were evaluated using Tukey's Studentised range test (Zar 1999, p. 210-214).

In Study III, the effects of block, site preparation, and yearly measurement on volumetric soil water content were tested. For each species, the effects of block (gradient position), site preparation and sowing date on seedling size and morphological characteristics were tested using a model for a split-plot design. All morphological characteristics, except specific root length and specific root surface area, were log-transformed (base-e log) for the analysis because the variances were positively correlated with the means (Zar 1999, p. 275). The effects of block and site preparation on soil properties and foliar N concentration were tested using analysis of variance. Multiple comparison testing was done using Tukey's studentised range test (Zar 1999, p. 210-214).

In Study IV, the effects of block, species, and moist chilling on seedling size and morphology were tested. Projected leaf area, aboveground dry biomass, height/stem dry biomass, needle length were log-transformed (base-e log). Because the amount of radiation seedlings received was autocorrelated to their location along the gap-understory gradient, which produced autocorrelation of the seedling variables data, partial Mantel statistics were used. Since the Mantel test is based on similarity or distance matrices (Mantel 1967), the partial Mantel statistic measures how well the variation in seedling size or morphology corresponds to the variation in radiation, while controlling for the effect of spatial location along the gap-edge zone. The effect of radiation on seedling size and morphology was analysed separately for each species and moist chilling treatment. In order to describe the spatial distribution of seedling variables and radiation, experimental data were spatially interpolated using geostatistical techniques, i.e. semivariance analysis and Kriging interpolation (Cressie 1989). First, experimental semivariograms were computed (Cressie 1993), then the exponential model was fitted to the experimental semivariograms. The fit of the models was relatively good ($r^2=0.76-0.95$, mean=0.90). Finally, maps of the spatial distribution of variables were drawn based on values obtained using Kriging interpolation (Rossi et al. 1992; Cressie 1993 p.105-209). Seedlings from both moist chilling treatments were combined to draw the maps of variables, since moist chilling was not a significant factor.

5. Results and discussion

5.1. Soil properties and moisture conditions

Because the variation in soil properties between blocks along the experimental area was large, results are presented by site preparation treatments.

For site preparation done in 1998, the top 6 cm of exposed E/B horizon contained more organic carbon and particles <0.06 mm than that of mounds and exposed C horizon, favouring a higher water retention capacity (Table 2 in Study III; Mecke and Ilvesniemi 1999; Mecke et al. 2000). Bulk density was higher on exposed C horizon than on exposed E/B horizon and mounds (Table 2 in Study III). Near saturated soil hydraulic conductivity (K_{11}) was lower on exposed E/B horizon ($0.22 \pm 0.11 \text{ cm h}^{-1}$) than on exposed C horizon ($0.92 \pm 0.71 \text{ cm h}^{-1}$). K_{11} was highest on mounds though variation between blocks was large ($3.36 \pm 3.63 \text{ cm h}^{-1}$). Accordingly, volumetric soil water content over the three growing seasons was highest on exposed E/B horizon (Table 3 in Study III). Such soil properties indicate that the water storage capacity of exposed C horizon would be low, particularly on blocks with single-grained coarse-textured soil where the lack of organic compounds and sesquioxides promotes a rapid percolation of soil water, and that the capacity would be increased on exposed E/B horizon where soil structure is intact (Mecke et al. 2002). These results support well the hypothesis that exposed E/B horizon retains more soil water than mounds or exposed C horizon.

For site preparation done in 1999, water retention at field capacity (Fig. 3 in Study I) and K_{11} were more variable between blocks, especially on exposed C horizon and mounds. This variability is presumably due to an irregular pattern of fine-textured lenses and layers in soil, which are typical for glaciofluvial deposits (Catt 1986). However, the soil water retention pattern at field capacity followed the trend for the content of fine soil particles (Fig. 3 in Study I; Mecke and Ilvesniemi 1999; Mecke et al. 2000). Apart from blocks containing fine-textured lenses and layers, volumetric soil water content was lowest on exposed C horizon, intermediate on mounds, and

highest on exposed E/B horizons (Fig. 2 in Study I and Table 3 in Study II). Discrepancies between volumetric soil water content and content of fine soil particles may originate from the fact that soil cores were not taken from the same location as the TDR probes were installed.

Yearly measurement, i.e. climate, affected volumetric soil water content (Tables 1 and 3 in Study III). Volumetric soil water content was almost the same with exposed C horizon, irrespective of the year, and was below the recommended lower soil water limit for seedlings (at -50 kPa matric suction, Table 2 in Study III; McDonald 1984). In comparison, the soil on mounds was moister on the rainy growing season of 1998 than on the dry growing seasons of 1999 and 2000, whereas the volumetric soil water content of exposed E/B horizon differed between all three years. On the dry growing seasons, volumetric soil water content of mounds did not differ from that of the single-grained coarse-textured soil of exposed C horizon, though it was higher on a wet growing season. The average volumetric soil water content of mounds and exposed E/B horizon was above the recommended lower soil water limit during the wet growing season of 1998, but not during the dry growing seasons of 1999 and 2000. Generally, volumetric soil water content of exposed C and E/B horizon was higher on blocks with fine- than with coarse-textured soil, and the difference was larger with exposed C horizon than exposed E/B horizon (not shown). Water storage of mounds was generally low and did not vary significantly between blocks.

The effect of climate was also reflected in the effect of sowing date on volumetric soil water content (Table 1 in Study I). In the moist and cool 1998 growing season, average relative humidity (RH) was 68% and air temperature (AT) was 8.9°C during the three-week period after the spring sowing; after the summer sowing, RH was 62% and AT was 14.7°C. In comparison, during the dry and warm 1999 growing season, RH and AT were 54% and 12.6°C after the spring sowing, and 53% and 16.9°C after the summer sowing, respectively. Consequent to weather conditions, soil water conditions at sowing time differed between sowing years. In both years, there was precipitation after the spring sowing, but a week without rain after the summer sowing (Fig. 2a in Study I). However, the difference in volumetric soil water content for the three-week period after the spring and summer sowings was significant in the dry growing season only (Table 1 in Study I). In both years, volumetric soil water content was highest on exposed E/B horizons and lowest on exposed C horizon though the difference was larger in the moist growing season than in the dry one (Fig. 2 in Study I).

Soil stabilisation did not affect any of the studied soil properties, except volumetric soil water content (Table 2 in Study II). Volumetric soil water content was usually higher on fresh site preparation treatments than on the corresponding stabilised ones (Fig. 4 in Study II). However, we should keep in mind that the effect of soil stabilisation on soil properties is confounded with the effect of climate (Pohtila 1977), especially since years were different in terms of precipitation. The effect of soil stabilisation is also dependent on the original properties of the soil, e.g. texture and organic matter content. Therefore, the experiment should be replicated over several years to obtain results that can be generalised.

Settling and compaction of soil were minimal after a time lapse of one year. This could be due to the fact that harvesting debris were removed before site preparation was done, such that mounds, where most re-arrangement in soil matrix is expected, rested against the ground, limiting the amount of settling. In addition, sample sizes (150 cm³) were small compared to the actual mound sizes. However, for

the water retention measurements, sample size was relatively large, such that the changes due to soil stabilisation that occurred at the soil surface (e.g. crust formation) were not reflected on the whole sample. Because we measured the difference in soil properties (for the comparison on the same soil as freshly prepared and stabilised) between the end of the first growing season and a variable time point during the second growing season, the full extent of soil settling is not known. Contrary to the results obtained, loss-on-ignition should be highest for mound soil, as they contained the most humus. However, because a good mound should be covered by at least 5 cm of mineral soil, little humus material from the broken O horizon was incorporated into the core soil sample taken from the top 6 cm layer of soil.

Soil aeration was not affected by site preparation. During all three growing seasons, the mean soil temperature ($12.2 \pm 1^\circ\text{C}$) did not vary between site preparation treatments or along the slope.

5.2. Seedling emergence

The emergence of *P. sylvestris* and *P. abies* seedlings was high in the moist growing season of 1998, but low in the dry season of 1999 (Fig. 4 and 5 in Study I). This may be due to climatic differences between years. In the moist growing season, the wet and cold soil in spring provided conditions that relieve seed dormancy (Gosling and Peace 1990; Jinks and Jones 1996), allowing the high and uniform emergence seen for both species. On the opposite, warm and dry weather shortly after the summer sowing in 1998 most probably caused the lower seedling emergence compared to the spring sowing. In the dry growing season, the lower emergence of *P. abies* compared to *P. sylvestris* after spring sowing when there had been little precipitation in the preceding month suggests that the emergence of *P. abies* seedlings is more sensitive to limited water supply than that of *P. sylvestris*. The decreased emergence of seedlings under dry and warm conditions agrees with earlier results for boreal conifer species (Yli-Vakkuri 1961a, b; Kinnunen 1982; Oleskog and Sahlén 2000).

Both growing seasons, mounds were most favourable and exposed C horizon least favourable to seedling emergence of *P. sylvestris* sown in spring. On the opposite, for the summer sowings, exposed C horizon was most favourable and exposed E/B horizons least favourable to seedling emergence (Fig. 4 and 5 in Study I). Surprisingly, emergence of *P. abies* was higher for the spring sowing during the moist growing season, but for the summer sowing in the dry growing season (Fig. 4 and 5 in Study I). Although site preparation and block (possibly the effect of soil texture and structure) affected volumetric soil water content and water retention capacity, they had only a minor effect on seedling emergence of both species when soil water and RH were high (Table 2 in Study I). In the moist growing season, precipitation and capillary water movement were able to keep the soil surface moist enough to fulfil the seeds' requirements for germination, as the evaporative loss into the humid air was low. In the dry growing season, a notable percentage of *P. sylvestris* seeds also developed into seedlings even though the soil was dry due to low precipitation and RH. Due to evaporation into the air, the water content of the soil in contact with the seeds was most likely lower than the water content 5 cm into the soil profile where measurements were made. Nevertheless, these field results agree with the laboratory results of Oleskog et al. (2000). The low emergence results of *P. abies* seedlings in the dry growing season suggest a sensitivity of this species to low soil water (Fig. 5 in Study I). In addition to low soil water, warm soil temperature may have decreased the germination rate and capacity of *P. abies*, especially since

temperatures higher than optimal affect *P. abies* more strongly than *P. sylvestris* (Bergsten 1989; Leinonen et al. 1993). For summer sowing in both years, daily maximum soil temperatures were over 25°C at a depth of 5 cm and thus higher at the soil surface (Kinnunen 1982; Grossnickle 2000).

The effect of soil stabilisation on seedling emergence was confounded by the effect of climate (Pohtila 1977). When emergence of seeds sown on the same site preparation plots but in different growing seasons is compared, the outcome of sowing was higher in the moist 1998 growing season when seeds were sown on fresh site preparation than in the dry 1999 growing season when sowings were done on stabilised site preparation (Table 3 and Fig. 5 in Study II). These results are most likely due to moister climatic conditions during the growing season when soil was freshly prepared than the following year when soil had stabilised. When comparing sowings done during the dry 1999 growing season on different fresh and stabilised site preparation plots, emergence was low for both species (Fig. 5 in Study II). Emergence of *P. sylvestris* was higher on stabilised than on freshly exposed C and E/B horizons, but was equally poor between fresh and stabilised mounds (Table 5 and Fig. 5 in Study II). One year of soil stabilisation did not affect significantly the emergence of *P. abies* (Table 5 and Fig. 5 in Study II). Seedling emergence, mortality, and establishment are affected by factors that vary yearly, such as drought, frost heaving, and predation; these factors confound the effect of soil stabilisation (Fleming and Mossa 1995). Therefore, the experiment should be replicated over several years to obtain results that can be generalised.

The seedling emergence results on the different types of site preparation treatments can be partly explained by the differences in hydraulic conductivity at –11 cm pressure head (K_{11}). Water moves slowly through the soil profile when K_{11} is low, e.g. on exposed E/B horizon, such that seeds can get enough water to imbibe and germinate. On the opposite, soil water quickly percolates down into the soil when K_{11} is high, such as on mounds where the humus (O horizon) content increased water infiltration (Ritari and Lähde 1978) and on the coarse-textured soil of exposed C horizon. Therefore, soil water conditions may not meet the requirements for seed germination when K_{11} is high, even though volumetric soil water content at 5 cm-depth may also be high. Accordingly, K_{11} may be as important as volumetric soil water content for seedling emergence. Because the measurement process of K_{11} is very laborious, measurements were conducted over an extended period of time during growing season 1999, and each replicate was measured only once during the study period. However, because soil properties changed as soil stabilised, the measurements may be biased due to temporal variation (Messing and Jarvis 1993, van Es et al. 1999). In fact, temporal variability within a growing season may affect water infiltration more significantly than soil properties and spatial variability (van Es et al. 1999).

5.3. Seedling mortality

5.3.1. First growing season

Predation and desiccation were the most common reasons for mortality during the first growing season. Mortality of *P. abies* was higher for spring-sown seedlings in the moist growing season, but for summer-sown seedlings in the dry growing season (Fig. 6 and 8 in Study I). The higher mortality for spring- than summer-sown seedlings in the moist growing season can be explained by the fact that spring-sown seedlings are exposed to predation for a longer time than summer-sown seedlings

(Vaartaja 1954), and because predation is higher in moist than dry growing seasons (Nystrand and Granström 1997). In the dry growing season, the recently emerged summer-sown seedlings were perhaps less resistant to summer drought than spring-sown seedlings (Jinks and Jones 1996). First growing season mortality of *P. sylvestris* was not affected significantly by sowing date.

For both species, first growing season mortality was not affected by site preparation or variation in soil texture and moisture (effect of block) when seeds were sown in the moist growing season (Table 3 in Study I). However, in the dry growing season, mortality of *P. sylvestris* was higher on exposed C horizon than on mounds (Table 3 and Fig. 8 in Study I). This result is in accordance with our hypothesis of limited water retention capacity of the exposed C horizon.

5.3.2. Winter mortality

Frost heaving, which may occur in autumn or in spring, was the main cause of mortality during the first winter (winter mortality is calculated as seedling death occurring outside the growing season). Frost heaving mortality was higher for *P. abies* than for *P. sylvestris*. The smaller root size of *P. abies* seedlings (Study III) may be a reason for their susceptibility to frost heaving (Goulet 1995). For the same reason, *P. sylvestris* and *P. abies* seedlings sown in the spring in the moist growing season were less affected by frost heaving than summer-sown seedlings, although this effect was not observed for seedlings sown in the dry growing season (Fig. 6 and 8 in Study I).

For seedlings of both species sown in the moist growing season and growing on mounds and exposed C horizon, mortality due to frost heaving was high and increased with an increasing content of fine soil particles (Fig. 6 and 7 in Study I). The high winter mortality of seedlings growing on mounds confirms earlier observations that greater soil disturbance, such as with mounding and ploughing, increase mortality due to frost heaving (Pohtila 1977, Örländer et al. 1990). The double humus layer under mineral soil in our mounds was not able to reduce capillary water movement and limit frost heaving damage, as suggested by Bergsten et al. (2001).

For both species, winter mortality was lowest on exposed E/B horizon (Fig. 6 in Study I). Moreover, with exposed E/B horizon on fine-textured soil, mortality due to frost heaving was close to zero, even though soil water content was high. Organic compounds and sesquioxides may reduce the risk of frost heaving by filling gaps between mineral grains and forming bridges between particles in the E and upper part of the B horizons, thus reducing the movement of soil particles when the soil freezes (Mecke et al. 2002). Our results are also supported by the laboratory results of Goulet (2000) who found that soil from the E horizon is less susceptible to frost heaving than soil from the Bs horizon. At our study site, the E horizon was thin (less than 1 cm) and easily destroyed by site preparation. This could explain the variation in seedling emergence and establishment on exposed E/B horizons, especially on coarse-textured soil where mortality was higher than on fine-textured soil, contrary to the other site preparation treatments. On coarse-textured soil, the differences in winter mortality between site preparation treatments were small.

It is noteworthy that soil stabilisation did not affect significantly seedling mortality due to frost heaving (Table 3 in Study II).

5.3.3. Second growing season and later

For seedlings sown in the moist growing season, second growing season mortality was high, especially on mounds and on fine-textured soil (Fig. 6 in Study I).

This result suggests that although seedlings survived the first winter, their roots may have been damaged by frost heaving, thereby making them more susceptible to desiccation during the second growing season (Goulet 1995). Second growing season mortality of *P. sylvestris* and *P. abies* seedlings was higher for the summer than for the spring sowing. However, for *P. abies* growing on mounds and exposed E/B horizon, the difference in mortality between sowings was small. These effects were not observed for seedlings sown in the dry growing season. Mortality was low during the second winter and the third growing season.

5.4. Seedling establishment

For sowings that took place in the moist growing season, the establishment of *P. sylvestris* and *P. abies* seedlings after three growing seasons was higher for the spring than for the summer sowing (Fig. 6 in Study I). For *P. sylvestris*, establishment was lower on mounds than on exposed E/B horizons, while establishment on exposed C horizon did not differ significantly from establishment on mounds or exposed E/B horizons. For *P. abies*, establishment was highest on exposed E/B horizons, intermediate on exposed C horizon, and lowest on mounds. In addition, establishment of *P. abies* on fine-textured soil was lower using mounds and exposed C horizon than with exposed E/B horizon. Establishment results did not vary much between site preparation treatments on coarse-textured soil. For the dry growing season sowings, establishment of *P. sylvestris* and *P. abies* after two growing seasons was low (Fig. 8 in Study I). Establishment of *P. sylvestris* was best on mounds for the spring sowing, but on exposed C horizon for the summer sowing, whereas establishment of *P. abies* was not affected significantly by any factor.

Direct and indirect effects of frost heaving largely explain the strong influence of soil properties and site preparation on establishment of seedlings in the moist growing season. On moist, fine-textured soil, mounding gave poor establishment results, contrary to results obtained by Mäkitalo (1999). However, our results agree with those of Pohtila (1977) and Pohtila and Pohjola (1985), who observed poor regeneration results using a combination of mounding and sowing. In the same way as for seedling emergence, the seedling establishment results can be partly explained by K_{11} and water retention of the site preparation treatments.

Similarly as for seedling emergence, the effect of soil stabilisation on seedling establishment is confounded with the effect of climate. When establishment of seedlings growing on the same site preparation plots but sown in different growing seasons is examined, seedling establishment was higher for seedlings sown on fresh site preparation (moist growing season) than on stabilised site preparation (dry growing season; Fig. 5 in Study II). When comparing sowings done during the same growing season but on different fresh and stabilised site preparation plots, establishment of *P. sylvestris* was higher on stabilised than on freshly exposed C and E/B horizons, but was equally low between fresh and stabilised mounds (Table 5 and Fig. 5 in Study II). In comparison, establishment of *P. abies* did not differ significantly between fresh and stabilised site preparation. Accordingly, it is not advantageous to wait for soil to stabilise before regenerating *P. abies* from seeds, though *P. sylvestris* could benefit from soil stabilisation, except when regenerating using mounds. However, the benefit of soil stabilisation has to be weighed against the risks of decreased seedbed receptivity and competition from vegetation.

5.5. Seedling morphological characteristics

5.5.1. Effect of sowing date

According to sowing dates, the difference in total growing season length between the spring- and summer-sown seedlings was only one month during the first growing season. However, because spring-sown seedlings were slower to emerge than summer-sown seedlings (Study I), the difference in total growing season length may in fact be shorter than one month for many seedlings, especially for *P. abies*. Nevertheless, three growing seasons later, spring-sown *P. sylvestris* seedlings were larger than summer-sown seedlings (Table 4 in Study III). Spring-sown *P. sylvestris* seedlings growing on exposed E/B horizon had more shoot dry biomass than summer-sown seedlings, whereas biomass did not vary between sowing dates for seedlings on exposed C horizon or mounds. Spring-sown *P. sylvestris* seedlings were taller than summer-sown seedlings, and had more total branch length. In addition, root dry biomass, length, and area of spring-sown *P. sylvestris* were larger than those of summer-sown seedlings. Spring-sown *P. abies* seedlings had more root dry biomass, longer roots, and more root surface area than summer-sown seedlings (Study III).

The results show that the benefits of sowing early were sustained for three growing seasons. However, the strong effect of sowing date on seedling size may in fact be a consequence of frost heaving root injuries that limited seedling growth on subsequent growing seasons (Goulet 1995).

5.5.2. Effect of site preparation

Contrary to the hypothesis that growth would be favoured by high water retention capacity, i.e. on exposed E/B horizon, *P. sylvestris* seedlings growing on mounds were the largest (Table 4 in Study III). Seedlings on mounds grew with their roots in humus, which provided a nutrient-rich substrate (Hallsby 1994, 1995). Consequently, foliar N concentration of spring-sown *P. sylvestris* seedlings was higher than the average foliar N concentration of nursery seedlings (1.4%, Jalkanen and Rikala 1995); in comparison, foliar N concentration of adult trees is 1.2% (Helmisaari 1991). As was shown by vector analysis (Fig. 2 in Study III), the high N uptake (content) of seedlings growing on mounds contributed to increase needle dry biomass. In addition, the high plant available N content (implied by a high foliar N concentration) contributed to increase branch production of *P. sylvestris* seedlings. Seedlings growing on mounds had low height/shoot dry biomass, which is typical of seedlings growing on soils with high N content (Will 1977). Another indication that seedlings on mounds had increased N availability is the fact that they allocated proportionally more biomass to the shoot than to the roots (Will 1977), i.e. they had high shoot/root dry biomass. However, a high shoot/root dry biomass may be a consequence of increased branchiness, as previously reported by Will (1977). Moreover, seedlings on mounds had short and thick roots, which is characteristic of N-rich soils (Bosemark 1954; Fitter 1985). Site preparation had a minimal effect on the morphology of *P. abies* seedlings, such that only the specific root length and specific root surface were affected.

According to our soil properties results, mounds were not the most fertile site preparation treatment as they did not contain the most organic C. Mounds were a heterogeneous growth substrate because they were roughly mixed during site preparation, and included humus and mineral soil. Accordingly, the location where soil measurements were made may not be representative of the location where seedlings actually grew. To a lesser extent, this is also true for seedlings growing on

exposed C and E/B horizon. In addition, soil measurements were performed on the top 6 cm of soil, whereas roots reached deeper into the soil after three growing seasons. Thus, seedlings on mounds could easily reach pockets of decomposing humus buried into the mineral soil. This could explain the discrepancies between soil properties data and seedling morphology results. The discrepancies may also indicate that other factors than those studied are more important to seedling development.

5.5.3. Effect of gap-edge zone

After two growing seasons, for a given amount of radiation received, *P. sylvestris* attained larger aboveground dry biomass, height, and projected leaf area than *P. abies* across the gap-edge zone (Fig. 3 and 4 in Study IV). The morphology of both species increased with increasing radiation, though the response was stronger for shade-intolerant *P. sylvestris* than for shade-tolerant *P. abies*. Mean needle length of *P. sylvestris* increased sharply with increasing radiation, while that of *P. abies* did not vary significantly with radiation. This shows that *P. sylvestris* has evolved a mechanism that allows it to increase its needle length with increasing radiation, contrary to *P. abies* which lacks this property. As a consequence, mean needle length contributed to the greater aboveground dry biomass and projected leaf area of *P. sylvestris* seedlings compared to those of *P. abies*. And accordingly, *P. sylvestris* allocated proportionally more dry biomass to needles than to the stem, i.e. to assimilating parts rather than to structural parts, with increasing radiation compared to *P. abies* seedlings, which did not show a significant response to radiation. A high biomass distribution to leaves means an increased potential for photosynthesis. The longer needles of *P. sylvestris* also contributed to increase its specific leaf area_p. A high specific leaf area provides more leaf surface to capture light while investing less in leaf biomass, thus enhancing relative growth rate (Reich et al. 1998; Wright and Westoby 2001). Specific leaf area_p did not differ significantly between species and decreased with increasing radiation, though the effect of radiation was significant for *P. sylvestris* only (Tables 1 and 2 in Study IV). Therefore, shade-intolerant *P. sylvestris* underwent changes that allowed it to capture more light than *P. abies*, both in the gap and under the canopy. As shade-intolerant *P. sylvestris* has a higher photosynthetic capacity than shade-tolerant *P. abies* (Ceulemans and Saugier 1991), *P. sylvestris* can compete for resources better than *P. abies*, and grow larger. However, high growth rates under the canopy have been shown to decrease seedling survival in the long run (Kobe et al. 1995).

The correlations between radiation and seedling aboveground dry biomass, height, and projected leaf area can be observed by comparing the maps displaying the spatial distributions over the experimental area (Fig. 2 and 4 in Study IV). The spatial pattern of radiation was relatively symmetrical in all directions, decreasing gradually towards gap edges from the maximum several metres north of the gap centre. Because of the asymmetric distribution of radiation in the gap and its surroundings, which is due to solar geometry at high latitudes, seedlings growing under the canopy at the northern edge of the gap received amounts of radiation that were similar to those received by seedlings growing in the southern part of the gap. In contrast, the spatial pattern of seedling size varied more in shape. In addition, the isopleths of radiation and seedling size variables were asymmetrical with the gap limits and converged to different locations. *P. sylvestris* reached their maximum size several metres northwest of the gap centre, southwest of the radiation maximum. From the peak value, the size of *P. sylvestris* decreased gradually towards the gap edges and into the forest. As a result of the asymmetric response of seedling size to the gap, the size of *P. sylvestris*

seedlings growing in the southern part of the gap was similar to that of seedlings growing under the canopy at the northern edge of the gap. The maximum size of *P. abies* seedlings was attained in the northern and northeastern parts of the gap. However, the response of *P. abies* to the gap and to increased radiation was not as strong as that of *P. sylvestris*. The area of maximum size attained by *P. abies* was diffuse and spread over the location of highest radiation. The isopleths of size of *P. abies* were more asymmetrical in relation to the gap limits than those of *P. sylvestris*.

If seedling size were affected solely by radiation, the spatial pattern of size variables would be equal along a same radiation level, whether located in the gap or under the canopy. However, with equal radiation, *P. sylvestris* seedling size varied more under the canopy at the northern edge of the gap than in the southern part of the gap. For *P. abies*, the opposite was true. This suggests that gap-edge zone characteristics other than radiation also influence seedling size. Apart from radiation, the development of seedlings is affected by other factors along the gap-edge zone, such as root competition for water and nutrients by ground vegetation and mature trees (Caldwell et al. 1995; Nilsson et al. 1996; Örländer et al. 1996; Jäderlund et al. 1997), and herbivory (Hulme 1996; Nystrand and Granström 2000). These effects, as well as early seedling growth, are likely to depend on within-gap position, since the competition of large trees retards the growth of ground vegetation at gap edges (Kuuluvainen et al. 1993). It is possible that these contrasting factors affecting seedling growth lead to some type of gap partitioning between species, as observed in previously published results (Wayne and Bazzaz 1993a, b; Bazzaz and Wayne 1994; Sipe and Bazzaz 1995; Gray and Spies 1996).

One should keep in mind that gap partitioning originates from different seedling survival rates in different parts of the gap, due to varying environmental conditions (radiation, water, nutrients, competition from grasses, etc). However, once seedlings are established, their growth is related to these same environmental conditions, such that *P. sylvestris* and *P. abies* may become dominant in different parts of the gap. Evidence of this was observed already after two growing seasons, with the largest *P. sylvestris* and *P. abies* seedlings found on opposite sides (east and west) of the location of highest radiation. The fact that seedlings grew better in some parts of the gap than others may also be due to interactions between the mineral seedbed and microclimate. For example, the western part receives most radiation in the morning when environmental conditions are most favourable for photosynthesis, i.e. when temperatures are low and relative humidity is high (Wayne and Bazzaz 1993a). Gap partitioning may become clearer after a longer regeneration period.

Differences in aboveground seedling size and morphology affect the abilities of each species for competition and establishment (Goulet and Bellefleur 1986; Zobel and Antos 1991; Tremmel and Bazzaz 1995). However, the overall competitive ability of a species is given by the combination of morphological strategy and physiological features. Although early development is important for establishment success, the physiological capacity (photosynthesis and respiration) of seedlings was not measured in this study. Consequently, our results cannot predict with certainty that *P. sylvestris* will outcompete *P. abies* in similar gap environments. Shade-intolerant *P. sylvestris* is more sensitive to shade and, therefore, may be less competitive than shade-tolerant *P. abies* at gap edges or in a shelterwood silvicultural system. In addition, *P. abies* is able to survive better than *P. sylvestris* when growing in the presence of competing vegetation (Jonsson 1999).

5.5.4. Effect of moist chilling

Although moist-chilled seeds germinated earlier than unchilled seeds (unpublished results), such that seedlings had a longer first growing season, the results show that moist chilling had a negligible effect on seedling morphology after two growing seasons. *P. sylvestris* and *P. abies* seedlings from moist-chilled seeds had lower specific leaf area_p than seedlings from unchilled seeds (Table 1 and Fig. 3d in Study IV). This result is in accord with Sellin and Fenner (2001), who reported that specific leaf area_p decreases with foliage age. Also, seedlings from unchilled seeds had higher height/stem dry biomass ratios than seedlings from moist-chilled seeds (Table 1 and Fig. 3f in Study IV). Having germinated earlier, seedlings from moist-chilled seeds may have begun diameter growth at the time of measurement, contrary to seedlings from unchilled seeds. Stem diameter growth implies increased stem dry biomass for a lower height/stem dry biomass ratio.

6. Conclusions and practical applications

According to the results of sowings done in the moist growing season, regeneration success was higher after the spring sowing, in terms of both seedling establishment and development. Summer-sown seedlings were more susceptible to frost heaving than spring-sown seedlings, and were exposed at early stages to dry and warm environmental conditions, which can cause drought. In addition, considering the sustained effect of sowing date on the size of *P. sylvestris* and *P. abies* seedlings after three growing seasons, it is advisable to sow seeds as early as possible in spring when regenerating forests through direct seeding. However, the strong effect of sowing date on seedling size may be a consequence of frost heaving injuries, which may have injured roots and limited seedling growth.

Site preparation, as well as soil texture and structure (the block effect), had only a minor effect on seedling emergence when environmental conditions were moist, though they had strong effects on volumetric soil water content and water retention capacity. When soil water and relative humidity were high, precipitation and capillary water movement kept the soil surface moist enough for germination. However, dry and warm weather had a negative impact on seedling emergence.

Based on the seedling establishment results of this study, site preparation methods that expose the E/B horizon should be used when regenerating sites using direct seeding or natural regeneration, especially on moist, fine-textured soils. Mounding and site preparation methods that expose the C horizon should be avoided, as these treatments had negative effects on soil water conditions that resulted in increased mortality when the growing season was dry. Because volumetric soil water content of exposed C horizon was always low, independently of growing season climate, this site preparation treatment should be used with caution, especially when regenerating sites with single-grained coarse-textured soil. In addition, seedlings growing on exposed C horizon were smallest. Furthermore, seedlings growing on mounds and exposed C horizon were prone to frost heaving, which was detrimental to seedling establishment, especially on moist, fine-textured soil. Nevertheless, from the point of view of seedling growth, mounds were the most favourable sites for the regeneration of *P. sylvestris* through direct seeding. Mounds were also favourable for root morphological characteristics of *P. abies* seedlings. Considering the above-mentioned factors and risks, exposed E/B horizon is a good alternative when regenerating *P. sylvestris* forests through direct seeding or natural regeneration.

No significant differences in soil properties between fresh and stabilised site preparation treatments were observed, indicating that a period of one year may be too

short to observe the effects of soil stabilisation. Nevertheless, soil stabilisation improved seedling emergence and establishment for *P. sylvestris* on exposed C and E/B horizons. Thus, *P. sylvestris* could benefit from soil stabilisation, except when regenerating using mounding site preparation. However, it is not advantageous to wait for soil to stabilise before regenerating *P. abies* from seeds. Mortality due to frost heaving did not differ significantly between freshly prepared and stabilised soil. In addition, leaving the soil to stabilise after site preparation may not be an economical alternative. The higher establishment of *P. sylvestris* seedlings on stabilised soil should be weighed against loss in seedbed receptivity. Further research is necessary to determine whether soil stabilisation would benefit seedling development as well.

During early development, shade-intolerant *P. sylvestris* seedlings underwent modifications that allowed it to capture more light and compete better for resources than shade-tolerant *P. abies* in gap and gap-edge environments. Aboveground dry biomass, height, and projected surface leaf area of both species increased with increasing radiation, but *P. sylvestris* responded more strongly than *P. abies*. In addition, *P. sylvestris* responded to radiation with a more flexible needle length than *P. abies*. Longer needles contributed to increase aboveground dry biomass, projected leaf area, and specific leaf area_p. Consequently, with increasing radiation *P. sylvestris* seedlings allocated proportionally more aboveground dry biomass to assimilating parts versus structural parts compared to *P. abies*. However, the lack of convergence between the spatial distributions of seedling size variables and radiation indicates that seedlings were also affected by environmental factors other than radiation. In addition, the asymmetric distributions of radiation and seedling size responses in relation to the circular gap imply that in order for seedlings to benefit optimally from radiation, gaps should have an elongated shape and a north-south orientation. This shape and orientation of gaps would maximise the area receiving the most radiation in the central part of the gap, while simultaneously minimising the area receiving the least radiation at the southern edge of the gap.

The establishment and development results reported in this thesis apply to the early stages of regeneration. Longer-term studies should be undertaken to determine whether the effects of site preparation, sowing date, soil stabilisation, and gap-edge zone on seedling establishment and development are sustained for several years. Even if these effects were not sustained, increased growth in the early stages of seedling development is important in order to promote the competitive ability of seedlings, to shorten the time it takes for seedlings to become dominant in relation to competing vegetation, and to reduce the risk of damage, e.g. by frost heaving or browsing. Seedlings growing on mounds have an increased advantage in competitiveness for radiation, being located above all ground vegetation. In contrast, seedlings on exposed C horizon are growing from a position below the level of competing vegetation, such that these seedlings may be in a shaded location when ground vegetation grows abundantly. These issues should also be considered when using site preparation treatments in small forest gaps in order to enhance the amount of radiation seedlings receive.

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