Interactions between Near-Ground Temperature and Radiation, Silvicultural Treatments and Frost Damage to Norway Spruce Seedlings

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Abstract

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Several different silvicultural treatments were studied in two experiments. In the first, mechanical scarification, slash removal, vegetation control, clear-cut age and seedling types were investigated with respect to frost injury to Norway spruce (*Picea abies* (L.) Karst.) seedlings. Frost damage was also related to near-ground minimum temperature. In the other experiment, the effects of Scots pine (*Pinus sylvestris* (L.)) shelterwood density gradients, ranging from dense, uncut forest to complete clear-cuttings, were analysed. Near-ground temperature and radiation were monitored close to planted Norway spruce cuttings with a mobile data acquisition system. Growth, frost damage and chlorophyll fluorescence were monitored and analysed in relation to microclimate. Budburst date was estimated and the nocturnal near-ground temperature during the period when the seedlings were most susceptible to frost was analysed in both experiments.

The shelterwood moderated near-ground radiation fluxes and diurnal temperature variations, while the daily mean temperature was unaffected. Near-ground minimum temperatures were lower, and vertical temperature inversions were more pronounced in clear-cuttings than in shelterwoods, during clear and calm nights. The effects were most pronounced during a dry period.

Budburst was delayed in the shelterwood. Later budburst was shown to reduce the risk of exposure to frosts during the most frost-susceptible period, when cuttings of two clones, differing in budburst date, were compared.

Mechanical scarification reduced frost damage to seedlings in the first growing season, but neither herbicide treatment, nor mowing affected the frequency of frost injury. The frequency of frost injury was higher amongst containerised seedlings than amongst bare-rooted seedlings, especially in the first growing season. Neither clear-cut age nor slash removal affected the frequency of frost damage. Frost injury to the cuttings was reduced by the shelterwoods, since 80% were damaged by frost in clear-cuts and low-density shelterwoods, 27% in moderately dense shelterwoods, and only 5% in dense shelterwoods. Of the climatic variables tested, the accumulated net and global radiation the day after a severe frost event were the most strongly correlated with the degree of frost injury among cuttings, and the variation in their F_v/F_m ratios, in the graduated shelterwoods.

Frost injuries were rarely lethal, but reduced growth and increased the proportion of seedlings with multiple leaders and spike knots, especially amongst seedlings that were repeatedly injured over several years. Height growth was lower in the clear-cut area than in moderately dense shelterwoods during years with severe frost damage.

Key words: Air temperature, Global radiation, Frost injury, Reforestation, Shelterwood, Scarification, Slash removal, Vegetation, *Picea abies*

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Consider a future device for individual use, which is a sort of mechanized private file and library. It needs a name, and to coin one at random, "memex" will do. A memex is a device in which an individual stores all his books, records, and communications, and which is mechanized so that it may be consulted with exceeding speed and flexibility. It is an enlarged intimate supplement to his memory.

It consists of a desk, and while it can presumably be operated from a distance, it is primarily the piece of furniture at which he works. On the top are slanting translucent screens, on which material can be projected for convenient reading. There is a keyboard, and sets of buttons and levers. Otherwise it looks like an ordinary desk.

- Vannevar Bush, As We May Think, Atlantic Monthly, July 1945

Contents

Appendix

Papers 1-4

This thesis is based on the following papers, which will be referred to by the corresponding Roman numerals.

I. Langvall O., Nilsson U., and Örlander G. Frost damage to planted Norway spruce seedlings — influence of site preparation and seedling type. For. Ecol. Manage. In press.

II. Örlander G., and Langvall O. 1993. The Asa shuttle — A system for mobile sampling of air temperature and radiation. Scand. J. For. Res. 8, 359–372.

III. Langvall O., and Ottosson Löfvenius M. Effect of shelterwood density on nocturnal near-ground temperature, frost injury risk and budburst date of Norway spruce. Manuscript.

IV. Langvall O., and Örlander G. Effects of pine shelterwoods on microclimate and frost damage to Norway spruce seedlings. Submitted manuscript.

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Introduction

Frost is defined as the condition that exists when the air temperature falls below 0°C (Rosenberg *et al.*, 1983). In all parts of the terrestrial landmass, except for lowland tropics, frost is a major concern, affecting the cultivation of agricultural, horticultural and silvicultural crops (Cohen, 1973; Bagdonas, 1978). Frost resistance varies greatly both amongst different plant species and amongst plants of the same species at different growth stages. Some coniferous tree species in the boreal forest can withstand very low temperatures, below –40°C, during winter, but can be damaged by temperatures just below ca –3°C during the sensitive flushing period in early summer (Perttu, 1981; Sachai and Larcher, 1987; Christersson and von Fircks, 1988; Gillies and Binder, 1997). Frost is a major limiting factor affecting the form and distribution of native vegetation (Rosenberg *et al.*, 1983). Even native vegetation can be strained by frost, and may cause reductions in stem growth, reduced quality or harvested volumes of crops, or even death. In forestry frost damage is mainly seen in regeneration failures, or in reduced growth and quality during regeneration phases of the rotations.

The timing and frequency of frost incidents vary according to several factors, including latitude, continentality, altitude, topography, vegetation cover, soil type and soil moisture. In forestry the microclimatic factors can be modified by silvicultural treatments. Another factor influencing the result of forest regeneration with respect to frost damage is the selection of plant material.

Climate

Latitude is a major underlying factor affecting the frequency and severity of frosts throughout the year. In boreal forests growth is concentrated in the summer, when daytime temperatures are high enough for photosynthesis and nocturnal temperatures seldom fall to damaging levels. Summer frost events are mainly restricted to nocturnal “radiation” frost, *i.e.* the type that occurs on clear and calm nights when the temperature falls below zero mainly through long-wave radiative energy losses (Figure 1). Regional and local variations greatly influence the risk of frosts during the growing season of the boreal forest. In areas close to the coasts and great lakes, the influence of the water bodies moderates the daily temperature fluctuations and, thus, these areas tend to have frost less often than interior and mountainous areas (Ångström, 1968; Perttu, 1981; Cohen, 1973). Locally, nocturnal temperature is greatly affected by topography. Low lying and flat areas, where the cold air accumulates during the night, have lower nocturnal temperatures than slopes and hilltops (Mattsson, 1978). Therefore a terrain model is often included in local frost risk modelling Mattsson, 1978; Laughlin and Kalma, 1990; Hess *et al.*, 1975; Kalma *et al.*, 1986, Blennow and Persson, 1998).

The energy balance at the soil surface determines the microclimate of the air near the ground. The main components of the energy balance are the net radiation, the

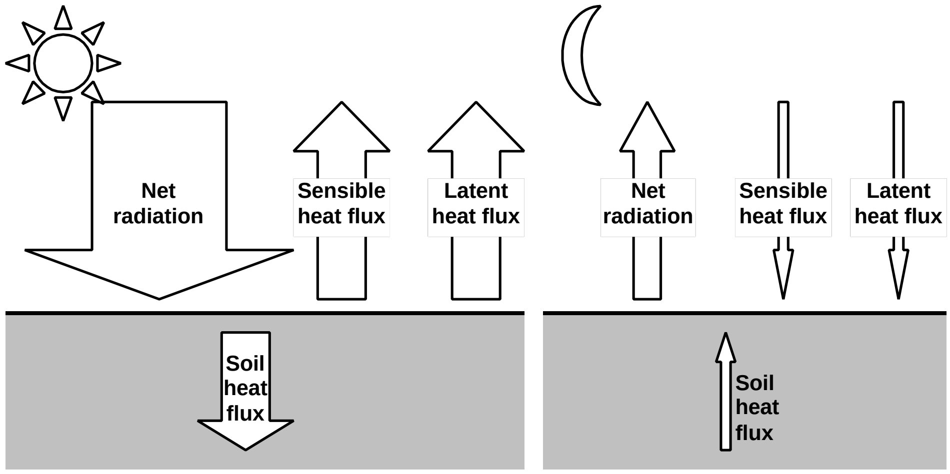

Figure 1. Energy balance of a clear-cut surface during sunny days (left) and clear and calm nights (right) (Oke, 1990).

turbulent latent and sensible heat fluxes, and soil heat flux (Figure 1). During a sunny day, the main energy source is the solar radiation, while energy is lost through turbulent latent and sensible heat, and stored in the soil. During a clear and calm night, the energy lost through radiation is partly compensated by energy from latent and sensible heat fluxes, and by released soil heat.

Nocturnal radiative energy loss in a clear-cutting depends on the difference between the soil surface temperature and the sky temperature, and the emissivity of the surface. The sky is colder during clear nights compared to overcast nights, so the radiative energy losses are higher. Below a canopy, the net radiation is reduced in proportion to the degree the sky is obscured by trunks and the canopy and, hence, radiative energy losses during clear nights are reduced (Perttu, 1981; Nunez and Bowman, 1986; Oke, 1990).

Turbulent heat transfer through sensible heat flux, *i.e.* transportation of warm air, is likely to be low during clear and calm nights at clear-cuttings. Temperature inversions normally develop, which have a restraining effect on vertical turbulent energy fluxes. Any turbulent mixing will raise the near-ground temperature since the cold air near the ground will be mixed with warmer air from higher levels. This effect is used in active frost protection, *e.g.* in fruit orchards, where wind machines, orchard heaters or hovering helicopters are sometimes used to mix the near-ground air (Ahrens, 1990; Bagdonas, 1978).

Turbulent heat transfer through latent heat flux (*i.e.* transportation of water vapour) on clear and calm nights in clear-cuttings, is evident when the temperature drops to the dew point temperature. Water vapour is then condensed to liquid phase (dew formation) or sublimated to the solid phase (ice formation) releasing heat to the soil surface. In moist air the nocturnal radiative losses are compensated by the greater release of latent heat, since the dew point is higher than for dry air, so the nocturnal air temperature can remain higher in moist conditions (Oke, 1990).

The soil heat flux is important for the energy balance at the soil surface during high-radiation nights in clear-cuttings, since the stored heat in the soil is an important energy source. The contribution from the soil depends on its thermal conductivity and capacity, especially in the uppermost soil layers. Mineral soil usually has high, whereas dry, poorly-humified peat has low, thermal conductivity and capacity. Water has high, and air low, thermal capacity and conductivity. Hence, a wet soil, where the volume of air in the soil is reduced, has higher thermal conductivity than a dry soil. Dry humus layers and dense ground vegetation also have lower thermal conductivity than soil and act as insulators, inhibiting the soil heat flux, and causing the air near the ground to be colder during high-radiation nights (Oke, 1990).

Frost injury

Plant tissue can withstand temperatures several degrees below zero before ice crystals form. The threshold freezing temperature, *i.e.* the highest temperature at which living plant tissues freeze, depends on cell sap concentration, state of maturity and degree of hardening. Freezing-sensitive tissues are immediately injured as soon as ice formation starts, while more freezing-tolerant tissues can withstand some degree of freezing, before the first injury appears (Sakai and Larcher, 1987). The resistance to freezing is lowest in flushing shoots. Norway spruce seedlings show evidence of freezing damage in flushing shoots when exposed to temperatures of about –3°C or lower (Day and Peace, 1934; Glerum, 1985; Christersson and von Fircks, 1988; Repo, 1992). The needles turn yellow or brown and the shoots droop within one or a few days. Even above lethal temperatures, the seedlings might sustain damage, especially to their photosynthetic systems, due to low temperatures (Strand and Lundmark, 1987; Lundmark *et al.*, 1988; Binder and Fielder, 1996a,b). Furthermore, the damage seems to be more serious if seedlings are exposed to excess light during the days following a night with frost (Lundmark and Hällgren, 1987; Örlander, 1993; Gillies and Binder, 1997). Photoinhibition occurs if the damage only temporarily reduces the photochemical efficiency of the chlorophyll, photodamage occurs if the exposure to light triggers oxidative processes associated with the chlorophyll, thus causing irreversible damage (Hällgren *et al.*, 1990). Photoinhibition, induced by low temperature, has been detected in coniferous seedlings by measuring the chlorophyll fluorescence, especially by monitoring the maximum photochemical efficiency of photosystem II as estimated from the ratio of variable to maximum fluorescence — the

F_v/F_m ratio (*e.g.* Binder and Fielder, 1996a,b; Lindgren and Hällgren, 1993; Örlander, 1993; Paper IV).

The sensitivity to low temperatures varies seasonally in boreal coniferous tree species (Figure 2; Sakai and Larcher, 1987). In winter they can withstand temperatures lower than –40°C. In spring the frost sensitivity gradually increases until budburst (Day and Peace, 1934; Repo, 1992). However, they are most sensitive during the initial period following budburst, when the shoots are 1–5 cm long (Dormling, 1982; Hannerz, 1994a; Bigras and Hebert, 1996). When the most intensive growth period has passed and the shoots start to differentiate, the frost hardiness improves (Andersson, 1968; Repo, 1992; Hannerz, 1994a) and in the autumn they become fully hardened again (Sakai and Larcher, 1987).

The period when the seedlings are most susceptible to frost, *i.e.* from budburst until the elongation of the shoot has finished, is of special interest. Frost injury to seedlings during this period often kills the flushing shoots, and is particularly severe when the terminal leader is killed. It is therefore important to define this period in relation to the between-year variation in the weather of the years studied. The nocturnal temperature during this period is more likely to reflect potential frost injuries to seedlings than it is at any other period, (such as the three summer months, the whole growing season or between any pair of fixed dates; Hannerz, 1999a). The temperature in spring is important for the timing of bud-

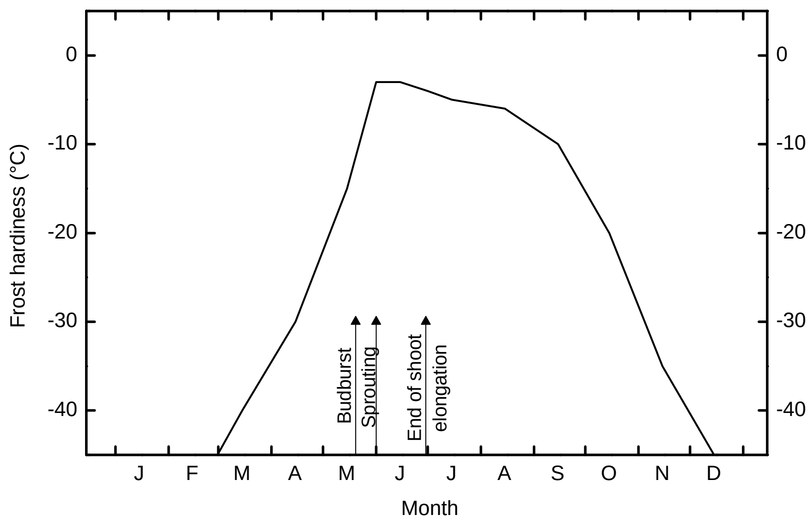

Figure 2. Generalised annual variation of frost hardiness and its relation to major phenological phases of buds/shoots of boreal conifers (after Day and Pearce 1934; Cannell and Sheppard, 1982; Sakai and Larcher, 1987; Hannerz, 1994a).

burst (Kozlowski *et al.*, 1991). Data on cumulative temperatures over a threshold value (*e.g.* +5°C), have been used to predict budburst in Sitka spruce and Norway spruce (Cannell *et al.*, 1985; Hannerz, 1994b, 1999a; Alfaro *et al.*, 2000). Genetic variation between provenances and individual seedlings with respect to heat sum requirements for budburst have also been reported (Cannell *et al.*, 1985; Hannerz, 1994b, 1999a; Papers I and III).

Frosts during the flushing period can reduce the height growth of seedlings by killing the terminal leader. Furthermore, the future wood quality of the trunk can also be substantially affected, since the risks of multiple leaders and spike knots forming on the seedlings increase, potentially reducing the profitability of the harvest (Klang, 2000).

Silvicultural treatments

Any treatment that affects the energy fluxes discussed above in a way that raises the nocturnal near-ground air temperature, can be used to protect the seedlings from frost during afforestation or regeneration of the forest.

Common practices in forest regeneration today include slash removal, soil scarification or removal of the ground vegetation in other ways, and leaving residual trees (shelter trees) to be cut after the new generation of seedlings has been established. Also, the time elapsed between cutting and planting can be an important factor in the regeneration procedure. These methods are often used for purposes other than frost protection, *e.g.* weed control, insect protection or to provide a source of seeds, but they can all also be effective, to a greater or lesser degree, in reducing the risk of frost damage to the seedlings.

Mechanical soil scarification can be beneficial for increasing the nocturnal temperature (Brække, 1972; Lundmark, 1982; Tolvanen and Kubin, 1990). Heat can be more easily transferred from lower levels to the soil surface following scarification, since insulating humus and vegetation is removed. Dense field vegetation can also dry out the upper soil, which further reduces the conductivity of the soil, and might therefore lower the nocturnal air temperature (Bärring, 1967; Davies, 1987). The more of the humus is removed, the more beneficial the treatment is likely to be. For example, Tolvanen and Kubin (1990) found that the lowest minimum temperature during the growing season was 1°C higher in scarified patches, 2°C higher following disc trenching and 2.6–3°C higher after ploughing, compared to unprepared soil. Complete soil tilling is, however, not practical in the stony soils in Sweden, except maybe on abandoned arable land. In modern forestry other environmental factors, *e.g.* nutrient leakage, biodiversity and historical factors, are also taken into consideration. Thus, the disturbed area of the soil surface needs to be reduced to a minimum. With mechanical scarification the micro-topography can also be altered. Mounds and berms offer planting spots that are somewhat elevated, and thus can reduce the risk of frost (Odin, 1964; Lundmark, 1987).

Other treatments which reduce the field vegetation, *e.g.* application of herbicide, mowing and steaming, could also be beneficial, but probably less so than mechanical scarification, since these treatments leave the humus layer undisturbed. The reverse could also be true, *i.e.* dense field vegetation could have a sheltering effect on small seedlings, protecting them from frost damage (Lundmark, 1982; LePage and Coates, 1994)

The effect of retained slash is unclear. Egnell *et al.* (1998) reported that frost damage to Norway spruce was slightly increased when slash was left on clear-cuttings. This was possibly an effect of reduced thermal conductivity. The slash could also act as a shelter, protecting small seedlings from frost damage, as described above.

In the first few years after cutting the field vegetation is often sparse, but after 2–3 years the ground is colonised and finally the whole area is usually covered by dense vegetation (Bergquist *at al.*, 1999). The humus layer may also start to be mineralised, and the thickness may be temporarily reduced (Lundmark, 1986). The time elapsed from cutting to planting might therefore affect the nocturnal temperature in the micro-environments of the newly planted seedlings.

Leaving a shelterwood is probably the most effective way to raise the nocturnal temperature near the forest floor (Ottosson Löfvenius, 1987, 1993; Groot and Carlsson, 1996; Odin *et al.*, 1984). The positive effect of residual trees is considered to be mainly due to reductions in the energy lost through radiation to the sky (Perttu, 1981; Nunez and Bowman, 1986). With increasing shelterwood density, the sky becomes increasingly obscured, and the out-going radiation is increasingly reduced (Reifsnyder and Lull, 1965). Other features of shelterwoods that generally raise the near-ground nocturnal temperature are their tendencies to increase air humidity, and soil surface moisture, while suppressing field vegetation. On the other hand, the shelter trees can dry out the soil, thus reducing heat conductivity. The reductions in short-wave radiation below the canopy during the day, caused by the shelterwood, also seem to reduce the risk of photoinhibition or photodamage to seedlings, after exposure to low temperatures (Lundmark and Hällgren, 1987; Örlander, 1993; Gillies and Binder, 1997). The reduced short-wave radiation will also reduce the seedling growth rates, to some degree (Groot, 1999; Örlander and Karlsson, 2000). However, provided the shelterwood is not too dense, this reduction could be less severe than the reduction that could be caused by frost injury if the area was clear-cut (Holgén and Hånell, 2000), if the area is prone to frost.

Late budburst reduces the risk of frost injuries by shifting the flushing period to a period with more favourable nocturnal air temperatures. Air and soil are normally warmer later in the summer, leading to higher heat fluxes and higher nocturnal air temperatures. The selection of a late-flushing provenance is regarded as one of the best strategies for avoiding frost damage (Cannell and Sheppard, 1982; Dormling, 1982; Hannerz, 1999b), since the average time between potentially damaging frosts is longer later in the season (Cannell *et al.*, 1985). Seedling age can also be important for the timing and length of the flushing period. Ununger *et al.* (1988) found that older seedlings flush later and have a shorter period of shoot elongation compared to young seedlings. This implies that planting older seedlings, which is often the case with bare-rooted seedlings, compared to containerised ones, could reduce the risk of frost damage. Furthermore, seedlings that establish more easily in the new environment after planting could flush earlier since they will tend to have better water uptake and metabolic functions. Lower rates of autumn frost damage among bare-rooted seedlings, compared to containerised ones, has been reported by Brække *et al.* (1986).

Objectives
The work described in this thesis was designed to evaluate the following interactions between near-ground temperature and radiation, silvicultural treatments and frost injury to Norway spruce seedlings: *i)* Near-ground temperature and radiation in relation to shelterwood density, ii*)* budburst and shoot elongation in relation to near-ground temperature, shelterwood density and seedling type, and *iii)* frost injury to Norway spruce in relation to near-ground temperature and radiation, shelterwood density, mechanical scarification, slash removal, vegetation control, clear-cutting age, and seedling type.

Material and methods

Location, design and aims of the experiments
This thesis is based on two experiments. In Experiment 1, frost damage to planted Norway spruce seedlings was studied in relation to near-ground temperature, site preparation, clear-cut age, slash removal, and seedling type. The effects of near-ground minimum temperatures during the budburst and shoot elongation period were also analysed (Paper I). In Experiment 2, the near-ground temperature and radiation regime in shelterwoods, and their effects on frost damage and budburst in Norway spruce cuttings were studied (Papers II, III and IV).

Experiment 1
This experiment was established at four sites in southern Sweden, at two coastal and two interior locations. Since frost damage was very rare at the coastal sites, only the interior sites, located in the Asa Experimental Forest, were used for the frost studies. However, one of the coastal sites was used in a bud development study, together with the interior sites.

Interior site 1 (Bråtarna) was located in a hilly area, with mesic soil and a sandy till. Interior site 2 (Lammhultsvägen) was located in an area with almost level ground with wet soil largely composed of fine sand covered with 10–20 cm of well-humified peat.

Each year during the 5-year period from 1989 through 1993, an area at each site was clear-cut. Each clear-cutting was divided into two parts of equal size, and the slash was removed from one part and retained on the other.

The experimental design comprised randomised blocks with subplots. Norway spruce seedlings, originating from the same seedlot, were planted in four blocks on each clear-cutting from the year it was cleared until 1993. Thus, in the areas that were cleared in 1989, plots were planted each year during the study period, while the areas cleared in 1993 were only planted in the year they were cleared. The blocks were equally distributed between the area cleared of slash and the area where the slash was retained.

Within each block, the area planted each year consisted of four site preparation treatment plots with 16 seedlings in each. Besides an untreated control plot, the treatments were *i)* repeated application of herbicide to the ground vegetation, *ii)* mechanical scarification (mounding), and *iii)* repeated mowing of the ground vegetation. The herbicide was applied so that the whole treatment plot was always free from ground vegetation, but the humus layer was left intact. At Interior site 1 the mounds were placed on mineral soil, whereas at Interior site 2 they were placed on upturned humus.

Norway spruce seedlings were planted around May 1st each year. Planted seedlings alternated between three-year-old bare-rooted seedlings and two-year-old containerised seedlings, except in 1991, when only bare-rooted seedlings were used. All seedlings used in this study were repeatedly treated with insecticide, to avoid insect damage.

Further details about the experiment are given in paper I.

Experiment 2

Experiment 2 was established in 1989 on almost level ground in the Asa Experimental Forest. In a dense, 70–90 year old, 25 m high mixed conifer forest stand, two plots were positioned and shaped so as to minimise the variation in the forest and the ground level. Plot 1 also included an area of abandoned arable land.

Each plot was partially cut in 1989, to create a shelterwood with a density gradient ranging from a dense forest (450 and 750 stems ha^{-1} in plots 1 and 2, respectively) to a clear-cutting, with intermediate densities of 320, 160, 80, 40, 20 and 10 stems ha^{-1}. Plot 2 was smaller in size than plot 1, and was therefore not used in the study described in paper III.

The plots were scarified (mounded) in the autumn of 1989. In May 1990 two clones of Norway spruce cuttings were planted in three rows along the shelter-wood gradients. One row was planted with cuttings of a single clone (C77-938, Hilleshög, Sweden) that, according to the suppliers, flushed five days later than the clone (C77-2009) planted in the other two rows. In total, 361 cuttings were planted in each row throughout the experimental area.

A few shelter trees (2% before 1993, and 8% in total) were windthrown or suffered die-back during the years following cutting, which slightly altered the microclimate at a few, small locations in the plots.

Further details can be found in papers II, III and IV.

Meteorological measurements

A climatic reference station has been collecting meteorological data at the research station in the Asa Experimental Forest from 1988 onwards. Daily minimum, mean and maximum air temperatures 1.7 m and 0.25 m above the ground, recorded by thermistors in ventilated shields at this station, have been used in these studies, in combination with climate measurements taken within the experimental areas.

In Experiment 1, microclimatic stations monitoring air temperature 1.7 and 0.3 m above the ground (unshielded copper-constantan thermocouples, wire ∅ 0.25 mm) were placed in the centre of the areas cut in 1989, 1991 and 1993 at each site. Daily mean and minimum temperatures were used in the analysis. For days for which climatic data from the experimental areas were missing, temperatures were estimated using regression functions (r^2>0.96) from climatic data measured by the reference station in Asa.

Experiment 2 included microclimatic monitoring below the canopy of a forest, which is more difficult than open-field measurements. The radiation, especially, can change dramatically within short time intervals, and the spatial distribution of both radiation and temperature varies with the irregular distribution and shape of tree crowns and variation in tree height. For reliable climatic estimations in time and space, many more samples are needed under a canopy, compared to an open field (Reifsnyder *et al.*, 1970). The data required were obtained using a mobile data acquisition system – the "Asa Shuttle", together with two stationary data-loggers. The shuttle was used for acquiring high-resolution data below the canopy, and the stationary data-loggers were used to collect data to test the accuracy of the measurements obtained by the shuttle, for wind monitoring and for climatic reference measurements during periods when the Asa shuttle was not running.

The Asa Shuttle (In Situ, Sweden) was designed to monitor air temperature at six levels above the ground (using unshielded copper-constantan thermocouples, wire ∅ 0.1 mm), air humidity (YA-100, Rotronic AG, Switzerland), photosynthetically active radiation (LI-190SZ, LiCor Inc., USA), net radiation (Q*4 and Q*6, Micromet Systems, USA), and global radiation (LI-200SZ, LiCor Inc., USA and CM5, Kipp&Zonen, The Netherlands) along the length of its rail. The CM5 global radiation sensor was attached for a week in 1990, for evaluation purposes. Naperian time constants were determined to <0.4 s for the thermocouples (according to functions derived by Blennow and Persson 1998), 10 µs for the LiCor sensors (LiCor Inc, USA), 4 s for CM5, 25 s for Q*4, and 23 s for Q*6. The thermocouples were ventilated by the movement of the shuttle (approx. 2 m s^{-1}).

The rail passed between two rows of planted cuttings. Measurements could be taken at any spot along the rail, while either standing still or running. Measurement points were selected so as to minimise the distance between pairs of cuttings planted on either side of the rail. All measurement points were measured while the shuttle was in motion except one, at which the shuttle stopped and waited for 30 seconds before the measurements were taken. This spot was the one closest to the stationary data-logger placed in the clear-cutting, and was used for evaluation purposes.

The shuttle was running during the growing seasons from May 1990 until June 1993. In all, 180 days were fully covered with measurements. Time series of daily minimum, mean and maximum air temperature measurements were needed in the analyses. For days for which data from the shuttle were missing, temperatures were estimated using regression functions correlating temperatures at the experimental site with data collected at the reference station in Asa.

Plant measurements

In Experiment 2, the diameter 1.3 m above the ground and height were measured of all the shelter trees every second year, and their geographical positions were determined with a surveying instrument in 1990.

The seedlings and the cuttings in the two experiments were measured every autumn. In addition to stem-base diameter and height, mortality and damage caused by frost were recorded. The severity of the frost damage was determined on a 6-level scale, from which the vitality of the whole seedling was estimated. In addition, frost damage to the cuttings in Experiment 2 were specifically studied on two occasions during the flushing period in connection with severe frost events that occurred during 18–20 May 1990 and 13–14 June 1993. The proportion of flushing shoots that were dead or drooping was determined for each cutting of the early-flushing clone. Flushing shoots on the entire cuttings were counted in 1990, while only shoots on the whorl of branches 15 cm above the ground were counted in 1993.

Wood quality-related properties of the cuttings were evaluated in Experiment 2 in the autumn of 1996. The diameter of the thickest branch was measured and the presence of multiple stems, multiple leaders and spike knots was registered.

Bud development and shoot elongation were thoroughly studied during the 1997 growing season among sub-samples of seedlings and cuttings in both experiments. In Experiment 1, the two interior sites and one of the coastal sites were used for this purpose, while cuttings of both clones were studied in Experiment 2. Twice a week during the period from May 15 to July 15, 1997, the developmental stage of one selected lateral bud per cutting was estimated, using definitions of bud development according to Krutzsch (1973). Bud development was also assessed on two occasions in 1991 and once in 1992 for all cuttings in Experiment 2.

Chlorophyll fluorescence parameters of needles of the cuttings in Experiment 2 were studied using a PSM Mark II fluorometer (Biomonitor S.C.I. AB, Sweden) during the 1990 growing season. To monitor the seasonal changes, measurements were carried out weekly, and to monitor changes resulting from low temperatures, further measurements were taken following the severe frost event that occurred during 18–20 May 1990. Measurements were carried out on one-year-old needles until June 12, after which they were done on current-year needles. The cuttings were naturally dark-adapted prior to the chlorophyll fluorescence measurements, since they were measured *in situ* at night. The F_v/F_m ratio of the chlorophyll fluorescence was used as an indicator of photoinhibition in this study.

Calculations

Temperature and radiation data preparation

Accumulated temperatures from 1 April onward were calculated for the year 1997 in order to relate them to the bud development studies in both experiments. In Experiment 1 the daily mean temperature 0.25 m above the ground was used, while the daily maximum temperature 1.7 m above the ground was accumulated in Experiment 2.

Minimum temperature, frost-day sum (the accumulated diurnal below zero minimum temperature) and the number of nights with frost were derived for the estimated frost-susceptible periods (see description below) for the investigated years.

In experiment 2, some of the shuttle data were recalculated. The height of the shuttle rail was adjusted every 6 meters and measurements were taken every second meter. Hence, the actual measurement height could slightly deviate from the nominal height (0.3, 0.4, 0.5 m etc.). The ground level was measured at each pair of planting spots, from which the true measurement heights of the sensors were determined, for each measurement point. Temperatures at the “true” height of 0.3 m were calculated using linear regression analysis of the readings from the thermocouple sensors at 0.3, 0.4 and 0.5 m nominal heights. Readings from sensors with time constants higher than the time passed between two measurement points (on average 1 s), *i.e.* the CM5, Q*4 and Q*6, were recalculated according to Perttu *et al.* (1977). The adjustments compensated for the fact that the sensors did not have time to equilibrate fully with the new environment when the sensors moved along the shelterwood transect.

The temperature regime in the shelterwood during clear and calm nights was studied in Experiment 2 (Paper III). A total of 32 nights in the growing seasons of 1990–1992 were selected for this investigation. The mean minimum temperature 0.4 m above the ground and the mean vertical minimum temperature difference between 1.7 m and 0.4 m above the ground were calculated for each measurement point along the shuttle rail. A dry period in 1992, during which the soil moisture was significantly lower than at other times, was represented by 10 of the selected nights, which were treated separately from the other nights.

Bud development analysis

In Experiment 1 the accumulated daily mean temperature 0.25 m above the ground was correlated to the bud development of the seedlings by linear regression. In Experiment 2 the accumulated daily maximum temperature 1.7 m above the ground was correlated to the bud development of the cuttings by subjectively interpolating the proportion of cuttings in different bud development stages between assessment dates. The period when the seedlings/cuttings were most susceptible to frost damage was defined as the period in which more than 5% of the seedlings/cuttings were in a frost-susceptible bud development stage. This, in turn was defined as the period from when the bud scales had burst and the tips of needles were emerging until shoot elongation had finished and the shoot had started to differentiate (index points 3–6; Krutzsch, 1973). The temperature sum requirements for the frost-susceptible period were determined for seedlings originating from the Maglehem seed orchard used in Experiment 1, and for each of the two clones used in Experiment 2.

With the accumulated temperatures from 1 April onward and the temperature sum requirements determined from the 1997 bud development studies, the dates for the beginning and end of the frost-susceptible periods were estimated for the studied years; 1990–1995 for Experiment 1 and 1990–1992 for Experiment 2. In Experiment 2 the periods were estimated individually for each cutting, since they experienced rather different maximum temperatures, depending on the density of the shelterwood surrounding them.

Statistical analysis

In Experiment 1 the frequency of frost-injured seedlings was determined for each plot and an analysis of variance for split-plot designs was used to statistically test the effects on frost damage of site, age of the clear-cutting, slash removal, site preparation and seedling type.

In Experiment 2 the microclimatic data and plant data were collected and analysed for each individual cutting. For clearance, the data were grouped, and means and SE were calculated for each group. In the study of the effects of shelterwood density on near-ground temperature, risk of frost injury and budburst date (Paper III), shelterwood density grouping was done with respect to the total basal area within a circular plot of 25 m radius, with the cutting in the middle. In the study of effects of shelterwoods on microclimate and frost damage (Paper IV), the grouping was done according to the total radiant energy received on a sunny day at the cutting level. The study included an investigation of photoinhibiton, which could then be directly related to the received radiation.

The frost event of 18–20 May 1990 was evaluated separately in Experiment 2 (Paper IV). Minimum temperatures 0.4 m and 1.7 m above the ground, accumulated hourly below-zero temperature, total time during which the temperature was below 0°C and –3°C, and cumulative negative net radiation were derived from the shuttle data for the night between May 19 and 20. Accumulated global radiation, total time during which global radiation exceeded 200, 400 and 600 W m^{-2} and accumulated positive net radiation were derived for May 20, the day after the frost event. In two separate multivariate data analyses, the derived climatic variables were correlated *i)* to the visual frost damage to the cuttings, and *ii)* to their chlorophyll fluorescence F_v/F_m ratios directly after the frost event.

Results

Mobile sampling of near-ground temperature and radiation

Single temperature readings taken by the Asa shuttle in motion were in good agreement with 10-minute mean temperatures obtained from the stationary measurement unit in the clear-cut area, although during daytime the readings from the shuttle fluctuated somewhat more.

The "true" measurement height only deviated slightly from the nominal height. For 85% of the measurement points, the deviation was less than ±5 cm. The difference between measured temperature at 0.3 m nominal height and the calculated temperature at 0.3 m "true" height was less than 0.1°C for most measurement points during clear and calm nights. The highest difference, 0.3°C, was found in the clear-cuttings. The difference was small compared to other temperature effects in the experimental area, and it was therefore considered not necessary to recalculate the temperature readings to true height in the following studies.

When comparing simultaneous temperature readings from the shuttle and the stationary data-logger in the clear-cutting, the shuttle gave on average 0.4°C higher values 0.3 m above the ground during the night. The mean daytime temperature was found to be equal for the two sensors, but individual readings could be ±2.5°C apart.

In another test, to identify possible radiation errors in the temperature readings, the temperatures at measurement points in full shade were compared to nearby points that were open to sunlight. A possible radiation error of 0.8°C was found.

When net radiation readings were adjusted for the reading errors, due to the long time constant, the values became independent of the direction the shuttle was moving. This indicated that calculated values were good estimates of the net radiation at each measurement point.

In August 1991, two types of pyranometer, a LI-200SZ and a CM5, simultaneously measured the global radiation in the shelterwood gradient. The LI-200SZ is not recommended by the manufacturer for measuring below canopies, but in this shelterwood no clear difference was found between the readings from the two types of instrument.

Microclimate

Near-ground air temperature

The air temperature was frequently below zero in the clear-cut areas during the period when seedlings/cuttings were most susceptible to frost. Sub-zero temperatures were most frequent on the sites on level ground, *i.e.* Interior site 2 of Experiment 1 and the clear-cut area in Experiment 2. The minimum temperatures and the accumulated diurnal minimum temperatures below zero, the frost-day sum, at these sites were lower (*i.e.* more strongly negative) than at the other sites.

The high shelterwood in Experiment 2 considerably moderated the diurnal temperature fluctuations during sunny days and clear and calm nights, but it did not alter the daily mean temperature as much (Figure 3). The maximum difference 0.4 m above the ground between the clear-cut and the dense forest was +4.5°C for the maximum, +0.7°C for the mean and –2.1°C for the minimum temperature. These figures refer to means of values obtained during 32 days and nights in 1990–1992.

During the period with a prolonged drought in 1992, the difference in minimum temperature between the open and the dense forest was more pronounced, and the vertical temperature gradient between 1.7 and 0.4 m above the ground was more than twice as high in the open areas, compared to periods with moist soil.

The number of nights with frost was lower and the frost-day sum was higher (*i.e.* less negative), the higher the density of the shelterwood.

Radiation

Radiation was only monitored in Experiment 2, where the canopy cover of the shelter trees could reduce the radiation flux near the ground.

On sunny days the global radiation reaching the forest floor in the most dense parts of the shelterwood was about 10% of the light level found in the middle of

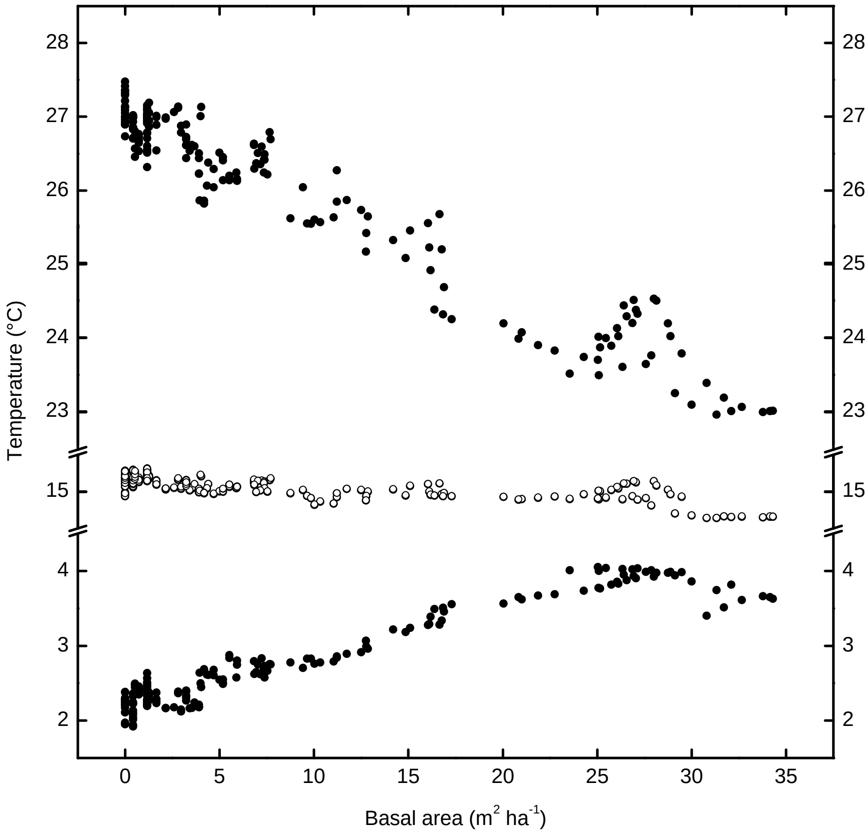

Figure 3. Average maximum (upper), mean (middle) and minimum (lower) temperature 0.4 m above the ground for 32 sunny days and clear and calm nights in 1990–1992 as functions of shelterwood density.

the clear-cut area, and the zone where 160 stems ha^{-1} had been left received about 60% of the clear-cut light level.

On a clear and calm night the net radiation at midnight varied from –1.8 W m^{-2} in the densest forest, to –42.7 W m^{-2} in the open.

Frost-susceptible periods

The temperature sums marking the beginning and end of the frost-susceptible period (during which at least 5% of the seedlings were estimated to be in a frost-susceptible bud development stage) for seedlings originating from the Maglehem seed orchard were 73 and 550 day-degrees, respectively. The requirements for individual seedlings varied widely, from 64 to 246 day-degrees for the start and 229 to 567 day-degrees for the end of the period. In Experiment 2, the accumulated maximum temperatures needed before 5% of the seedlings started flushing were 249 and 298 day-degrees for the early- and late-flushing clones, respectively, and 596 and 656 day-degrees, respectively, for the end of the frost-susceptible period. The individual differences in temperature sum requirements for the single-clone-cuttings were small, about 50 day-degrees for the start and 160 day-degrees for the finish.

The differences in temperature sum requirements led to differences in the estimated mean budburst date during 1990–1992, from May 15 for the Maglehem seedlings, through May 21 for clone 2009 to May 26 for clone 938 in clear-cut areas. The finishing dates of the frost-susceptible period varied from June 24 for clone 2009, through June 30 for clone 938, to July 14 for the seedlings. Furthermore, the shelterwood delayed the start and finish of the frost-susceptible period. In 1990–1992, the estimated start of the period was delayed on average 10 days and the end of the period on average 11 days in the densest part of the shelterwood (30–35 m^2 ha^{-1}).

Frost injury and silvicultural treatments

Seedlings planted in mounds after scarification had a significantly lower frequency of frost injuries, compared to seedlings planted in undisturbed humus in the first growing season. The other vegetation control treatments tested, herbicide application and mowing the ground vegetation, had no significant effect on frost injury to the seedlings.

The frequency of frost injury among containerised seedlings was higher than among bare-rooted seedlings. The difference between the two types of seedling was most pronounced in the first growing season, and declined during the following two years.

The age of the clear-cutting at the time of planting did not affect the frequency of frost injured seedlings, neither did removal of the slash.

The two experiments indicate that the choice of origin of the seedlings is important for the risk of frost injury. The relatively early-flushing seedlings originating from the Maglehem seed orchard had higher frequencies of frost injury in Interior site 2, compared to the two clones used in the nearby clear-cut areas in Experiment 2, every year between 1991 and 1995. Furthermore, the early-flushing clone had more than twice as many injured cuttings as the late-flushing clone.

Leaving a shelterwood had the most pronounced effect on frost damage of the tested silvicultural treatments. On average 80% of the cuttings planted in the clear-cut areas and low-density shelterwoods were injured by frost, but only 27% and 5% were injured in moderately dense and dense shelterwoods, respectively,

Table 1. Frost injured cuttings in experiment 2 during the growing seasons 1991–1997 and 1999, divided into three shelterwood basal area classes

Year	Frost injured cuttings (%)				Proportion of severely injured cuttings (%)
	0–10 $m^2 ha^{-1}$	10–20 $m^2 ha^{-1}$	20–35 $m^2 ha^{-1}$	Total	
1991	17	14	4	13	1.1
1992	10	4	0	7	2.1
1993	87	32	5	66	27.4
1994	82	19	1	60	0.0
1995	90	24	2	67	3.5
1996	63	32	13	51	4.7
1997	0	0	0	0	
1999	0	0	0	0	

during 1993–1996 (Table 1). In 1993, the year in which the most severe frosts occurred, the frequency of cuttings with severe frost injury in dense shelterwoods (with 40–60% of full light levels) was reduced to 3%, and in the densest parts (<40% light level) to zero, compared to 18% of the cuttings planted in the open (80–100% light level).

Photoinhibition after exposure to low nocturnal temperatures was detected in 1-year-old needles of the cuttings in Experiment 2. This applied especially to cuttings in the open parts of the shelterwood and the clear-cutting (80–100% light level), where the mean chlorophyll fluorescence F_v/F_m ratio decreased from 0.74 prior to a frost event, to 0.49 after the frost event. No change in the F_v/F_m ratio was found in the densest parts of the shelterwood (<40% light level).

All tested climatic variables, except minimum temperature 1.7 m above the ground, were correlated to the variation in frost injury and the F_v/F_m ratio of the cuttings in the shelterwoods, when tested in the multivariate data analysis. However, the climatic factors which were most strongly correlated to frost injury and F_v/F_m ratios were the accumulated positive net radiation and global radiation the day after the severe frost event.

Seedling mortality and growth

In most cases the frost damage did not immediately kill the injured seedlings, but reduced their growth rates.

In Experiment 1 only three out of 7680 seedlings were judged to have been killed by frost, and in Experiment 2 none was considered to have died because of frost injuries. Even so, the overall mortality was found to be higher among seedlings

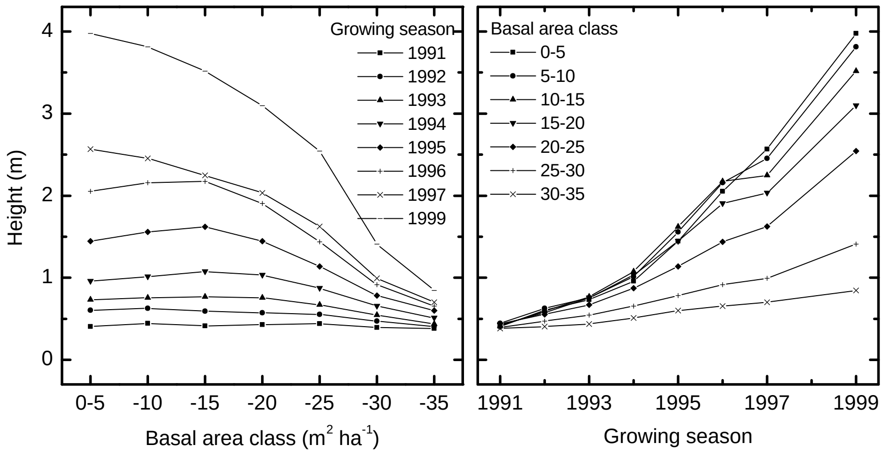

Figure 4. Height of Norway spruce seedlings as a function of shelterwood density (left), and development of height as a function of time, in different shelterwood densities (right).

that had been previously injured by frost on one site in Experiment 1. In the shelterwood experiment, 42 cuttings out of 724 died in the first 10 years. Of these, 45% were planted in the clear-cutting or the open shelterwoods (basal area 0–5 m^2 ha^{-1}) and 55% were planted in shelterwoods denser than 20 m^2 ha^{-1} basal area. In the moderately dense shelterwoods (basal area 5–20 m^2 ha^{-1}) all cuttings survived. For 86% of the dead cuttings, the cause of death could not be determined with certainty.

Frost injured seedlings showed reduced stem volumes, compared to undamaged seedlings in Experiment 1. For seedlings injured in several different years, the reduction was even more pronounced. In Experiment 2, the growth of the cuttings was correlated with the light levels they experienced at their respective planting spots, in the first three years (Figure 4). From 1993 through 1996 more of the cuttings in the open areas (basal area 0–5 m^2 ha^{-1}) were frost injured (Table 1), and thus had lower growth rates, compared to cuttings in the moderately dense shelterwoods (5–15 m^2 ha^{-1}; Figure 4). After 1996 no frost injuries were recorded, and consequently, growth accelerated in the open areas. Height growth was also set back in 1996, especially in the moderately dense shelterwoods (5–20 m^2 ha^{-1}, Figure 4), due to an attack by the fungus *Gremmeniella abietina* (data not shown).

The assessment of wood quality-related properties in Experiment 2 in 1996 showed that the highest proportion of cuttings with multiple stems, multiple leaders or spike knots was found among the cuttings that had been injured by frost in several different years. For cuttings that had been injured by frost in five or more years, 16% had multiple stems, 24% had multiple leaders, and 75% had spike knots. Corresponding values for cuttings that did not have any registered frost injuries over the years were 3%, 5% and 7%, respectively. The thickest branches were found in the open areas (0-5 m^2 ha^{-1}), where the average diameter of the thickest branch was 14 mm, compared to 10 mm in dense shelterwoods (15-25 m^2 ha^{-1}).

Discussion

Mobile sampling of temperature and radiation

In this study, radiation was monitored below the canopies of the shelterwoods, using a mobile sampling technique. The technique of directly measuring light levels below the canopy with fixed sensors has been used in previous studies, such as Ottosson Löfvenius (1993) and Machado and Reich (1999). However, since a large number of samples are needed for accurate estimates of radiation below canopies (Reifsnyder *et al.*, 1970), the mobile sampling technique is superior for this purpose (*cf.* Brown, 1973; Péch, 1986; Chason *et al.*, 1991). Indirect techniques of estimating radiation below canopies have also been used, *e.g.* hemispherical photography (*e.g.* Reifsnyder and Lull, 1965; Blennow *et al.*, 1998; Blennow, 1995) and hemispherical sensors (*e.g.* LAI-2000, LiCor Inc, USA; Machado and Reich, 1999). However, when total short-wave or daytime all-wave net radiation is estimated, the solar path has to be modelled when using these techniques (*cf.* Ottosson Löfvenius, 1993; Blennow *et al.*, 1998). Furthermore, the openness of the canopy might change during the season or between seasons, and these factors have to be considered.

Air temperature below the canopy was also monitored by mobile sampling. Mobile sampling of air temperature has been used in local-scale studies of temperature variation, together with GIS data (*e.g.* Blennow and Persson, 1998; Söderström, 2000), but not in micro-scale below-canopy temperature monitoring. The temperature variation below the shelterwood was found to be moderate compared to the variation in the clear-cut area in this study (Paper III), so the principal benefit of the mobile air temperature sampling in this case was that instantaneous readings of both radiation and temperature from the same sample points were obtained.

A major advantage of the mobile sampling technique was that only one set of sensors was needed. Thus it was more economical, with fewer instruments to calibrate, and readings from different parts of the shelterwood were directly comparable without calibration. Furthermore, the spatial resolution could be very high (0.2–0.3 m for the Asa shuttle) without incurring higher costs, and temperature sensors were automatically ventilated by their movement, reducing the reading errors when radiation was high.

Some disadvantages with mobile sampling were also identified. For instance, the spatial distribution could only be evaluated in one horizontal dimension (along the rail), measurements were not simultaneous for different sample points, only single values were obtained, and it was difficult to maintain long time series of data since operational failure was more common for the mobile unit, compared to the stationary data-loggers. Furthermore, some factors were difficult or impossible to sample with the shuttle, *e.g.* wind speed, wind direction, soil temperature and soil moisture. The general problem of using sensors with long time constants was overcome by recalculating data according to Perttu *et al.* (1977), and therefore presented no significant obstacle. One difficulty throughout the years has been that very large amounts of data have been collected by the mobile sampling. The data collected over approx. 250 days by the Asa shuttle resulted in a ca 2GB database, with 11 million records! However, the disadvantages were found to be minor compared to the benefits the mobile sampling technique offered.

Microclimate during forest regeneration

Clear-cutting is an extreme phase in the rotation of a forest, with respect to the near-ground climate. The clear-cut area have a high risk of nocturnal frosts during the active growth period, but in other respects offer good growth conditions.

In Experiment 1, both regional and local climate variations were observed (Paper I). The coastal sites were the mildest, and Interior site 2, on level ground, was the most frost prone site, in accordance with findings of various authors, such as Perttu (1981). The temperature conditions varied considerably between years, and seedlings at the moderately frost prone site (Interior site 1) had a relatively small risk of frost damage. On the highly frost prone sites (Interior site 1 in Experiment 1 and the clear-cut area in Experiment 2) seedlings frequently experienced temperatures below zero during the active growth period, and almost every year the minimum temperature reached damaging levels (Papers I and III).

The moisture in the superficial soil layers was found to be an important factor affecting the harshness of the nocturnal temperature in the clear-cuttings (Paper III). When the soil dried out during a long drought period, the minimum temperature and the vertical minimum temperature gradient became larger, indicating an increased nocturnal radiative energy loss. Brække (1972) also reported lower near-ground minimum temperatures over peat land, where the ground water table was lower. The thermal conductivity of the soil probably decreased due to the drought and thus reduced the soil heat flux from lower strata to the surface (Oke, 1990; Geiger *et al.*, 1995).

The shelterwood offered more variation in the microclimate than clear-cuttings (Paper III). As expected, the variation was density dependent; the higher the density, the stronger the moderating effect on temperature found during clear and calm nights, in accordance with earlier studies (Odin *et al.*, 1984; Ottosson Löfvenius, 1993; Groot and Carlson, 1996; Blennow, 1998). The shelterwood also clearly lowered the maximum temperature during sunny days. Since the daytime and night-time effects were reversed, the daily mean temperature was almost independent of the shelterwood density. Ottosson Löfvenius and Odin (1991) found similar variations in minimum, mean, and maximum temperatures between clear-cuttings and shelterwoods in several studies in Southern Sweden. They also found that the vertical temperature gradient, the inversion, gradually decreased with increasing shelterwood density, in accordance with findings in Experiment 2 (Paper III).

All radiative fluxes, net all-wave, global and photosynthetically active radiation, were moderated by the shelterwood. Daily total energy fluxes have been used in this study, but the spatial and temporal variation in short distances and time periods, respectively, could also be analysed from the data, thus, further exploring the radiative characteristics of the shelterwood with variable density.

The reduced light conditions of the shelterwood, especially in the densest parts, reduced the height growth of the seedlings. Similar reductions have been recorded for Norway spruce advance growth in the same shelterwood (Örlander and Karlsson, 2000) and for planted white spruce seedlings elsewhere (Groot, 1999).

The active growth period

Using accumulated temperatures above a threshold value, the most active growth period was estimated for Norway spruce seedlings, and thus the period when the seedlings were most susceptible to frost damage was identified (Papers I and III). For seedlings growing on clear-cuttings in Experiment 1, the daily mean temperature sum above +5°C was used, which has been used in earlier studies of budburst (Hannerz, 1994b, 1999a; Cannell *et al.*, 1985; Alfaro *et al.*, 2000). However, the daily maximum temperature sum above +10°C was used in Experiment 2, in an adjustment of the method to suit the shelterwood environment. The accumulated daily mean temperature did not satisfactorily reflect the accumulated heat sum required for budburst when comparing clear-cut conditions with the more moderate daily temperature fluctuations found in the shelterwood. In the bud development assessments in 1991 and 1992 in the shelterwood, the delay in budburst was found to be positively correlated to the density of the shelterwood (Paper III), but the daily mean temperature did not vary accordingly (*cf.* Figure 3). Kozlowski *et al.* (1991) thought that many heat sum studies were limited, because they assumed a constant relationship between temperature and growth during all stages of plant growth and during the day and night. The results in Paper III indicate that daytime temperature, as indicated by the daily maximum temperature, is more important for budburst of Norway spruce seedlings than the night-time temperature. Maximum temperature sum has earlier been used by Jonsson (1969) with respect to the budburst of Norway spruce and Scots pine (see Odin *et al.*, 1983).

The importance of choosing seeds with appropriate origins was obvious when comparing the mean dates of the start and end of the frost-susceptible periods for the Maglehem seedlings (Paper I) and the two clones used for the cuttings (Paper III). The frost-susceptible period for individual seedlings varied greatly within the genetically variable population of the seedlings. Thus, selecting late-flushing individuals in breeding programmes, as suggested by authors like Hannerz (1999b), could be an important strategy for avoiding frost damage.

The shelterwood effect on budburst timing was comparatively high in this study. Groot and Carlson (1996) found a maximum, non-significant, delay of two days in the budburst of white spruce, and no difference amongst trembling aspen saplings. The year-to-year variation in the number of days the budburst was delayed was high, ranging from four days in 1992 to 14 days in 1991 in the study in Paper III. Groot and Carlson only examined the budburst in 1994, which may have been a year with small differences, compared to the average, or the budburst could be more homogeneous in Ontario, due to its more continental climate. Furthermore, the use of single-clone cuttings seemed to be advantageous when studying bud development, since they have more constant flushing patterns compared to seedlings (*cf.* Papers I and III), leading to lower standard errors in the statistical tests.

Normally, the frequency of nights with frost is higher early in the season, even in years with high day-time temperatures in the spring and early budburst. Nocturnal temperatures during the frost-susceptible period in this study (Paper I) tended to be harsher, with higher frequencies of nights with frost, lower minimum temperatures and frost-day sums, during years when the flushing was early. The same tendency was found when comparing temperature conditions experienced by the early-flushing clone with the late-flushing clone during their respective active growth periods (Paper III). Similar trends were also noted by Cannell *et al.* (1985), who reported that the average time between frosts ≤ –2.5°C at the date of budburst, were longer for genotypes of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) with late budburst. In the shelterwood, the combined effect of higher nocturnal temperatures and delayed flushing led to considerably lower frequencies of nights with frost and reductions in the frost-day sum in the dense parts of the shelterwood, compared to the clear-cut area (Paper III).

The susceptibility to frost damage is highest during the active growth period (Sakai and Larcher, 1987). For Norway spruce the lowest temperature that can be tolerated during this period is reported to be about –3°C (*e.g.* Day and Peace, 1934; Christersson and von Fircks, 1988; Repo, 1992). In the study reported in paper I, visible frost injuries were found even during years when the lowest measured minimum temperature was as high as –0.8°C. Due to the high spatial variations in minimum temperatures that occur in clear-cuttings (*cf.* Blennow, 1998; Paper III), some of the seedlings might have experienced lower temperatures than measured at the climate station in the middle of the clear-cutting. In the study described in paper IV, visible frost injuries (>20% of the flushing shoots damaged) were first found on cuttings experiencing –3.2°C in the clear-cut area, while in the dense shelterwood cuttings experienced –4°C without serious damage during a severe frost event. Thus, the shading of the latter cuttings apparently increased their tolerance to low temperatures (*cf.* Örlander, 1993).

Frost injury in relation to silvicultural treatments

Leaving a shelterwood was found to be the single silvicultural treatment that most improved the microclimate, with respect to reducing the risk of frost damage to the seedlings (*cf.* Ottosson Löfvenius, 1993; Groot and Carlsson, 1996). Thus, the shelterwoods efficiently reduced the frost injuries to Norway spruce seedlings, in accordance with previous studies, such as Holgén and Hånell (2000). The "shelterwood effect" was found to be multidimensional since nocturnal temperatures remain high, while reducing net radiation, global radiation and periods of intense light the day after severe frost events. All of these effects were negatively correlated to visual frost damage (Paper IV). Furthermore, by delaying the frost-susceptible period, the shelterwoods reduced the cuttings' risk of exposure to sub-zero temperatures when in a susceptible developmental state (Paper III).

The analysis of wood quality-related properties showed evidence of decreased risk of stem defects on trees if seedlings were protected from frost by a shelterwood. Klang and Ekö (1999) found in a study in Southern Sweden that the proportion of planted Norway spruce seedlings with stem defects was 37% under shelterwoods compared to 50% in clear-cuttings. They also stated that 65% of the defects were related to frost damage. Thus, a reduction in wood-quality-related defects might increase the future value of the forest, even if volume growth might be reduced below a shelterwood (Klang, 2000).

Mechanical scarification also significantly affected the level of frost injury, but the effect was fairly small, compared to the shelterwood effects (Paper I). In this study, the scarified mounds were rather small and therefore the relatively small effect on frost damage observed was expected. Other authors have reported high temperature effects of scarification (*e.g.* Brække, 1972; Lundmark, 1987; Tolvanen and Kubin, 1990), but the proportion of scarified area needs to be considerably larger than it was in this study, before there is likely to be a significant effect on the heat balance in the area (*cf.* Brække, 1972; Tolvanen and Kubin, 1990).

Other vegetation control treatments tested, *i.e.* application of herbicide and mowing, did not significantly affect frost damage (Paper I). Dense, high-growing grass-dominated vegetation has been reported to reduce the heat transfer between soil and air (Hogg and Leiffers, 1991). On the sites used in this study, the vegetation was dominated by Hairy grass, *Deschampsia flexuosa* (Bergquist *et al.*, 1999), which seemed to have an insignificant effect on the surface energy balance. An indication of this was that there were no significant differences in soil temperature at 10 cm depth between plots with intact ground vegetation and plots treated either by herbicide or mowing, as earlier reported from the same experiment by Nilsson and Örlander (1999).

Slash removal did not have any significant effect on frost damage in this study. Egnell *et al* (1998) also reported that slash only had minor effects on the risk of frost injury.

Containerised seedlings were more frequently damaged by frost than bare-rooted seedlings (Paper I). Similar differences in frost damage between seedling types as a result of autumn frosts have been reported by Brække *et al.* (1986). Higher growth rates among containerised seedlings in the first years after planting reported by Nilsson and Örlander (1999) from Experiment 1, indicate that they establish faster, which may lead to earlier flushing. The difference in flushing dates may also have been due to differences in the ages of the two seedling types, since the containerised and bare-rooted seedlings were two and three years old, respectively. Ununger *et al.* (1988) reported an age-effect on flushing that was most pronounced in the first two growing seasons, but they found no differences after the fourth season. In our study, the first season in the field was the third and fourth growing season since germination for the containerised and bare-rooted seedlings, respectively, so the age-effect on them should have been small.

The time elapsed between cutting and planting did not affect the frequency of frost damage (Paper I). Ottosson Löfvenius (1993) reported a gradual decrease in temperature gradient between 1.7 and 0.25 m above the ground in the years following clear-cutting, which indicates that the risk of frost may decrease over time. On the other hand, the invading field vegetation would tend to increase the risk of frost. However, since no effect was found of herbicide or mowing treatments in this study, the vegetation found here was not likely to increase the risk of frost damage over the years.

Conclusions

A shelterwood can reduce the risk of frost injury to Norway spruce seedlings by *i)* reducing near-ground radiation fluxes, *ii)* increasing near-ground temperatures and reducing vertical temperature gradients on clear and calm nights, and *iii)* delaying budburst, compared to conditions in clear-cuttings. The optimal density of a shelterwood should be chosen with respect to the desired reduction of the frost injury risk and the desired rate of seedling growth.

Other treatments that reduce the frost injury risk include mechanical scarification, choosing seedlings with late budburst, and using older, bare-rooted seedlings.

Frost injuries to Norway spruce seedlings can *i)* reduce height and volume growth, *ii)* increase wood-quality-related defects, and *iii)* increase the risk of mortality in the long term by reducing vitality.

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