Regeneration under shelterwood - control of environmental factors

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Abstract

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The objectives of this work were to quantify the effects of stand stem density (SSD), orientation and distance with respect to shelter tree, and fertilisation on the establishment of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. regenerated by direct seeding and planting at different soil preparations. The field experiments were performed on South (64°14'N, 19°46'E, 225 m a.s.l.) and North (64°09'N, 19°36'E, 274 m a.s.l.) slopes in boreal Sweden. Regeneration and early growth in three stand stem densities (SSD's) with different light regimes, i.e. uncut forest (~500 stems/ha), shelterwood (~150 stems/ha), and clear-cut, were compared. Sowing, after using two soil preparations (mineral soil and a mixture of mineral soil and humus layer ground to a fine texture), and planting were done in 2001 at six distances in north-south direction from trees (0.5, 1, 1.5, 2, 4 and 6 meters). Naturally regenerated *P. abies* seedling and saplings were also selected in pairs in the uncut forest. Half of all seedlings and saplings in the experiments were irrigated with fertiliser (10mM N).

The light environment didn't differ significantly between different orientations or distances with respect to trees, but it was clearly different between SSD's. On the North slope, the emergence of direct seeded seedlings was highest (50 in percent of germinable seeds for *P. sylvestris* and 44% for *P. abies*) in SSD 150. On the other hand, on the South slope the conditions in SSD 0 favoured the high emergence of *P. sylvestris* (41%). Only for *P. abies* on the North slope, fertilised seeded seedlings were taller (ca. 20%) than non-fertilised seeded seedlings after 4 years. For planted *P. abies,* the fertilised seedlings in SSD 0 were the ones that grew the most (22.2 cm). Fertilisation had no effect on height growth of planted *P. sylvestris*, but the growth was clearly increasing (from <20 cm to >50 cm) with decreasing SSD. The naturally regenerated seedlings/saplings in the different height classes showed no response in height growth to fertilisation. With planted *P. sylvestris* being the more extreme, dry mass of leading shoot in SSD 500 was only 3% of that in SSD 0, while for height growth the corresponding value was almost 30%.

The main conclusion was that for plant establishment the general conditions of the stand mattered more than the orientation and distance with respect to the nearest tree and the light environment was more important than the nutritional status, i.e. light requirements could not be moderated by nutrient supply. A resulting new hypothesis was that a system of forest gaps and shelterwood in a geometric pattern could be used in conventional forestry to regenerate forests. This new method of Continuous Cover Forestry (CCF) would benefit from shelter trees while creating the desirable conditions of a clear-cut.

Keywords: Biomass, Direct seeding, Frost heaving, Fertilisation, Height growth, Light, Predation, Shelterwood, Soil preparation, Clear-cut, Dense forest

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Om man aldrig vågar göra det man tror att man inte kan,
kommer man aldrig att få veta vad man kan göra.

Charlotta

Contents

List of papers

This licentiate thesis summarises and discusses the following two papers, which will be referred to by their respective roman numerals.

I. Erefur, C., Bergsten, U. & de Chantal, M. Establishment of direct seeded seedlings of Norway spruce and Scots pine: effects of stand conditions, orientation and distance with respect to shelter tree, and fertilisation. Submitted.

II. Erefur, C., Bergsten, U., Lundmark, T. & de Chantal, M. Establishment of planted seedlings of Norway spruce and Scots pine: effects of stand conditions, orientation and distance with respect to shelter tree, and fertilisation. Manuscript.

Introduction

Alteration of stand structure influences the ecosystem

The structure of a forest has a direct bearing on the energy, hydrology and nutrient cycles within a forest ecosystem. An alteration of stand structure will influence the functioning of the ecosystem and there will be a direct effect on site microclimate, water balance, and soil fertility and therefore a direct influence on the physiological response of seedlings (Grossnickle, 2000).

A shift in energy balance occurs when there is removal of the forest canopy (Oke, 1987). A much higher amount of radiant energy will reach the soil surface. This change in energy distribution clearly alters the temperature of soil and air, as well as the evaporative requirements near the ground (Grossnickle, 2000). A mature forest stand has a rather high transpiration rate and that gives a reduced and regulated stream flow through the ecosystem. The energy balance also influences snow conditions. The hydrological cycle is dramatically altered in a clear-cut, which is characterized by low stand transpiration, increased stream flow, and potentially high amount of available soil water (Ibid.). The amount of soil water available for seedling emergence and establishment also depends on the texture and structure of the soil. In climax forests nutrient cycling is slow since most nutrients are bound in the biomass or organic matter on the ground. The removal of biomass through harvesting reduces the nutrient content of the site and the remains come foremost from the forest floor and are rapidly being cycled through decomposition and mineralization (Ibid.).

The conifers of the boreal forest are no exceptions to being influenced by many different factors during establishment and growth, as well as during germination and plant formation (de Chantal *et al.*, 2003a, b, 2004; Goulet, 1995; Oleskog *et al.*, 2000; Oleskog & Sahlén, 2000a; Oleskog & Sahlén, 2000b; Winsa, 1995b; Winsa & Sahlén, 2001). Specific conditions will differ depending on the site and stand environment, i.e., the light, water and nutrient conditions, and the plant material.

Partial forest canopy retention systems

In areas that are difficult to regenerate, for example in wetlands, in areas with high risk of frost, or in stands where competition from the surrounding vegetation is severe, the use of shelterwoods, i.e. a form of Continuous Cover Forestry Systems (CCFS), when regenerating forests can be advantageous. Shelter trees not only provide seeds for natural regeneration, but they could also create a favourable environment for seedlings. The ground temperature in a day is more stable in a shelterwood than on a clear-cut since the overstorey trees to some extent prevent the long-wave radiation from leaving to the atmosphere. This will give less frequent summer frosts and frost heaving but also less incoming radiation (Hannerz & Gemmel, 1994; Örlander & Karlsson, 2000; Örlander & Langvall, 1997). Other effects of shelter trees are that the seedlings will benefit from less wind exposure, more stable soil water content (on a clear-cut there can easily be an excess of water when the mature stand is removed, but also droughts as a result of more extreme temperatures), and less vegetation competition for seedlings (Holgen & Hånell, 2000).

Already in the middle of the 19th century a debate about regular and irregular silviculture started in Europe. This has lead to the present CCFS's which involve the maintenance of a forest canopy during the regeneration phase. Clear-felling of areas much more than two tree heights wide without the retention of some mature trees is avoided (Mason, Kerr & Simpson, 1999). The idea behind contemporary CCF is to provide more diverse forests for multi-purpose benefits and the adoption of CCFS on any scale will require changes in both silvicultural practices and management thinking. It does not mean abandoning stand management or timber production, though. CCF is more than a silvicultural system, it is one approach to forest management (Mason, Kerr & Simpson, 1999).

Some of the advantages of CCF are less visual impact than with clear-felling, and increased within-stand structural and species diversity. With CCF there are fewer disturbances of the forest ecosystem and greater abundance of sheltered microsites for regenerating seedlings. There are usually reduced regeneration costs and higher production of large diameter and high quality logs (Mason, Kerr & Simpson, 1999). CCF can complement conventional forestry methods in the Nordic counties by favouring ecological, cultural and social factors. This is especially interesting in Sweden since ecology and socio-cultural factors have as equal or almost as equal importance as economy in the Swedish forest policies (cf. Anon., 1993).

Factors affecting establishment

Natural conditions provide environmental heterogeneity both in space and time since there is daily as well as annual variation. The effect of variation at these different scales depends on the plant's rate of response to physiological and ecological processes of interest. Each seedling experiences fluctuations and individual acclimation may be an important component of response and performance through time. Additionally, species also differ in their rate of response to environmental changes and the phenotypic plasticity of an individual has a strong influence on how the scale of environmental fluctuations influences the whole plant performance, i.e., growth, survival and reproductive output (Ackerly & Bazzaz, 1995). For example, in forest gaps, individuals located on the west side receive more light in the morning hours when CO_2 levels are high and tissue water potential is less negative. The plant can then photosynthesize at a high rate. In contrast, plants located on the east side of the gap receive sunlight mainly in the afternoon, when

CO_2 levels are no longer high and plant tissue water potential has become more negative. In the latter case, resource processing can be greatly reduced depending on the ability of the plant to hold and protect resources until other essential resources become available (Bazzaz & Grace, 1997). Transient sun patches in the understorey of a forest provide bursts of high energy that are critical for carbon gain in these environments. The utilization of this energy depends on the duration of the sun patch because various physiological processes, like photosynthesis, stomatal opening and enzyme activity, respond at different rates to a change in radiation environment (Ackerly & Bazzaz, 1995). Whole plant carbon gain depends on the temporal scale of diurnal fluctuations in light environments, even when the total amount of light is constant (Wayne & Bazzaz, 1993).

Important components of plant response to closure in forests and gap creation are physiological and allocation responses to fluctuating light environments on longer time scales (Ackerly & Bazzaz, 1995). Features like the activity of myccorhizas (Jentschke, Godbold & Brandes, 2001), competition within the neighbourhood of a tree (Malcom & Ibrahim, 1993), soil temperature which controls nitrogen mineralization (Domisch *et al*., 2002), or fertilisation and irrigation treatments (Albough *et al*., 1998; Ingerslev & Hallbäcken, 1999) are of big importance for allocation patterns and should not be forgotten in this context.

As well as abiotic factors, there are biotic factors like predation on tree seeds and seedlings which have a big impact on establishment. According to Nystrand and Granström (2000), seedling predation on *P. sylvestris* is negatively related to stand disturbance. They compared uncut forest, shelterwood, and clear-cut. Seed predation on the other hand, decreased in the order shelterwood>uncut forest>clear-cut. There was generally large between-site variation for predation, though. The most important seed predators were carabids, while juvenile seedlings were predated mainly by slugs.

Plant material

An important factor influencing the choice of silvicultural system is the light requirement of the species to be regenerated. Shade tolerant species can be expected to grow in small gaps of 0.05 ha or even less (Mason, Kerr & Simpson, 1999). Intermediate species can grow under canopy, but for good seedling growth a rather rapid canopy removal is required. Light-demanding species will require very light canopies or open areas to achieve adequate growth. All species can occur as advance regeneration underneath an overstorey, but if the seedling is not shade tolerant enough it will not be able to survive and grow for any length of time.

In the same way as a natural forest has a distribution of gap sizes, a managed forest subjected to silvicultural treatments can have a gap size distribution. Habitat conditions vary among gaps, within gaps, at gap edges, and within the forest stand matrix (Coates & Burton, 1997). The climate of the forest is overall very complex. Big openings are exposed to a higher amount of shortwave radiation, more extreme changes in temperature between night and day, higher ground temperature and greater wind speeds than a closed forest (Geiger, 1995). The microclimate and local climate affect seedlings and trees as well as forest stands directly or indirectly to a very large extent. The chances for survival and growth of an individual depend on the local climatic conditions.

The establishment, growth and development of trees all interact strongly with the physical environment. For different plant material and phases of seed/seedling development, stand type and site conditions together with the location of seedlings compared to the surrounding trees create different light, water and nutritional statuses, as well as risk for/benefits of mechanical disturbances (such as rain/snow and predation). Better understanding of these interactions is necessary to improve our capability to predict how the productivity and development of forest ecosystems will respond to natural disturbances, climate change and forest management. Prediction of the effects of silvicultural manipulations must be based on the spatial as well as temporal dynamics of forest responses to different kinds, sizes, frequencies and intensities of disturbances (Coates & Burton, 1997). Successful strategies must be based on an understanding of interactions among shelter, vegetation, the physical environment, and the response of regenerating tree species.

Objectives

The overall aim of this thesis is to quantify and describe the response of different plants to different/contrasting growing environments and try to understand how the environment can be moderated in combination with the plant material to get a cost-effective regeneration of forests under shelterwood, i.e. in CCFS's.

In specific, the objectives of Paper I were to quantify the effects of stand stem density (SSD), orientation and distance with respect to shelter tree, and fertilisation, on seedling emergence, mortality, and early growth of *P. abies* (*Picea abies* L. Karst.) and *P. sylvestris* (*Pinus sylvestris* L.) by direct seeding at different soil preparations. The overall hypothesis was that light would be the main explanatory factor, therefore one further objective was to characterise the light environment in the different SSD's.

The objectives of Paper II were to quantify the effects of SSD, orientation and distance with respect to shelter tree, and fertilisation on early height growth and biomass allocation of planted *P. abies* and *P. sylvestris* seedlings. The effect of fertilisation on growth of naturally regenerated *P. abies* seedlings and saplings in uncut forest was also tested.

Material & Methods

Study sites and experimental design

The experiments were performed on a South slope (64°14’N, 19°46’E, 225 m a.s.l., 7.5% declination) and a North slope (64°09’N, 19°36’E, 274 m a.s.l., 12% declination) in Vindeln Experimental Forests, 60km NW of Umeå in northern Sweden. Both slopes are spruce-dominated with a vegetation cover dominated by *Vaccinium myrtillus* L. on a moist podzolic soil with a texture of loamy sandy (till). For further information on the site characteristics and the climate conditions during the years of the experiments, see Paper I (Table 1 and 2). Three different types of stands were selected/created at each site, that is SSD 500 (~500 stems/ha, i.e. uncut forest), SSD 150 (~150 stems/ha, i.e. thinned forest or shelterwood) and SSD 0 (clear-cut).

The same experimental design was used on both slopes (Figure 1, I; Figure 1, II). Five shelter trees were selected in SSD 500 and SSD 150. In SSD 0, the locations of two hypothetical trees were marked with sticks. Two opposite blocks were delimited in the north-south direction from each selected (or hypothetical) tree. In each block, two sets of six parcels (40 × 100 cm each) separated by at least 20 cm were marked at distances of 0.5, 1, 1.5, 2, 4 and 6 meters from the shelter tree. No other tree was closer to the parcels than the selected shelter tree except at distances of 4 m (in SSD 500) and 6 meters (in SSD 150 and 500).

Paper I

Each parcel was divided in two subparcels. Seedbeds were prepared using two soil preparations, HuMinMix and bare mineral soil, that were randomly allocated to each subparcel. HuMinMix, i.e. a mixture of humus layer and mineral soil ground to a fine texture (47% average loss on ignition on the South slope and 66% on the North slope), was done mechanically using a rototiller mounted on a clearing saw (Winsa, 1995b). To improve emergence, micropreparation was done manually before sowing with a tool (8 × 22 cm) consisting of 10 adjacent inverted square pyramids (5 × 2 pyramids, each 4 × 4 cm and 2 cm deep) that make indentations in the seedbed to improve capillarity and thus seedling emergence (Winsa & Bergsten, 1994). The tool was pressed twice on each subparcel to create two series of 10 indentations. Ten seeds each of were sown in each subparcel (one species per series of indentations, randomly allocated). The seeds used in this study originated from Scots pine (Östteg 65°1’N) and Norway spruce (Hissjö 64°1’N) seed orchards, with germination capacities of 96.2% and 97.3%, respectively.

Paper II

In each parcel four seedlings, two of *P. abies* and two of *P. sylvestris*, were planted at least 20 cm apart. The location of species within the parcels was randomly selected. The plant material of this study was one-year-old containerised *P. sylvestris* and *P. abies* seedlings originating from Östteg 65°1'N and Hissjö 64°1'N, respectively. Fifteen pairs of naturally regenerated *P. abies* seedlings/saplings in three different height classes, i.e. <0.5 m, 0.5-1 m, and >1 m (5 pairs in each class), were selected in SSD 500. They were selected to represent seedlings/saplings in an average light environment of SSD 500, i.e. not being too close to a mature tree.

From each pair of parcels at each specific distance and in each direction from the selected (or hypothetical) shelter trees, one was randomly chosen to be fertilised. Fertilisation was performed every other week during June, July and August 2002-2004 for the direct seeded seedlings. A water solution of N, P and K (10 mM N) was showered onto the seedlings, giving a total amount of at least 0.09 g of nitrogen per season and seedling. Half of all planted (one parcel at each specific distance and in each direction from the selected shelter trees) and naturally regenerated (one of each pair) seedlings and saplings were also fertilised, with the same fertiliser and technique but every other week during June, July and August 2001-2004. The total amounts of nitrogen given were for the planted seedlings 0.56 g per seedling in 2001 and 0.34 g of nitrogen per seedling in 2002-2004, and for the naturally regenerated seedlings and saplings 2.24 g in 2001and 1.34 g in 2002-2004 for seedlings <0.5 m, 4.48 g versus 2.73 g for seedlings 0.5-1 m, and 6.72 versus 4.20 g for saplings >1 m.

Inventories

Paper I

Inventories were done in July 2001-2003 and at the end of the growing season from 2001 to 2004. Exceptionally, an inventory was done also in the spring of the second growing season (2002). During these inventories, all emerged (2001) or surviving (2002-2004) seedlings were recorded, as well as injury and mortality due to predation, frost heaving, physiological and mechanical damage, and mortality due to unknown causes. Height was measured from the root scar/soil surface to the tip of the terminal bud at the end of each growing season.

Paper II

Inventories recording height and length of leading shoot as well as status of the seedling were done at the end of the growing season each year from 2001 to 2004. Height was measured from the root scar/soil surface to the tip of the terminal bud and length of leading shoot was measured as the growth of the current year for the shoot having apical dominance to the tip of the terminal bud. Status was graded depending on physiological or mechanical damages, such as effect of water stress, frost, fungi, or browsing. For the naturally regenerated seedlings and saplings, height and length of leading shoot were measured at the end of the growing season each year from 2001 to 2004. At each inventory status of the seedling or sapling was also recorded. In October/November 2004 the seedlings were destructively sampled for biomass, meaning that after they were measured for the above mentioned characteristics, they were cut at the soil surface and divided into the three different fractions of stem, twigs, and leading shoot. For a number of seedlings randomly selected at 0.5, 2, and 6 meters from trees in the SSD's, roots were also sampled.

Fish-eye photos

The light environment in the different SSD's was characterised by the total site factor (TSF), i.e. the relative amount of incidental (direct + diffuse) photosynthetic photon flux density (PPFD) that penetrates below canopy for a specified period of time. To do this, fish-eye photos were taken during totally or partly overcast days in July 2006. Photos were taken at a distance of 1.25 and 5m north and south of the selected shelter trees. In SSD 0 a photo was taken at the point of each hypothetical shelter tree (i.e. two photos from each slope). The photos were analyzed using Regent Instruments computer software WinSCANOPY (2005) with the pixel classification done in grey scale and the time for growing season set as June 1-September 30.

Statistical analysis

The effects of SSD, orientation and distance in relation to tree, soil preparation, and fertilisation, as well as their interactions, were tested for each species and slope using analysis of variance (MiniTab GLM; Anon 2000). Using all SSD's in the data, all dependent variables were tested for all factors of relevance, except for orientation and distance in relation to tree, and their interactions with each other and other relevant factors, which were tested without using SSD 0. This was because in SSD 0, orientation and distance in relation to tree are only hypothetical factors of the design. Differences were considered significant at $p \leq 0.05$. When significant effects were found, Dunett's and Tukey's multiple comparison tests were used to test differences between treatments. The height growth of the naturally regenerated seedlings during the four years of the experiment was analysed using Minitab's paired t-tests with a confidence interval of 95% for mean differences (Anon, 2000).

Results & Discussion

Light environment

An average for both slopes showed close to homogenous light environment within each SSD, but clearly different environments between SSD's, with less than 20% of PPFD above the canopy reaching the forest floor, i.e. being transmitted, in SSD 500, 40% in SSD 150, and 80% in SSD 0 (I; Figure 1). No significant differences were found between the different orientations or distances with respect to tree. In accordance with this, orientation and distance with respect to tree and had generally no effect on growth for this plant material and in these SSD's. Ottosson Löfvenius (1993) came up with the same result of no actual spatial variation in global radiation in a shelterwood of 43 stems per hectare. With lower SSD's, and in pine forest, Strand et. al. (2006) and Elfving and Jakobsson (2006) have shown positive correlation between increased distance to nearest shelter tree and growth of seedlings/saplings and trees, respectively.

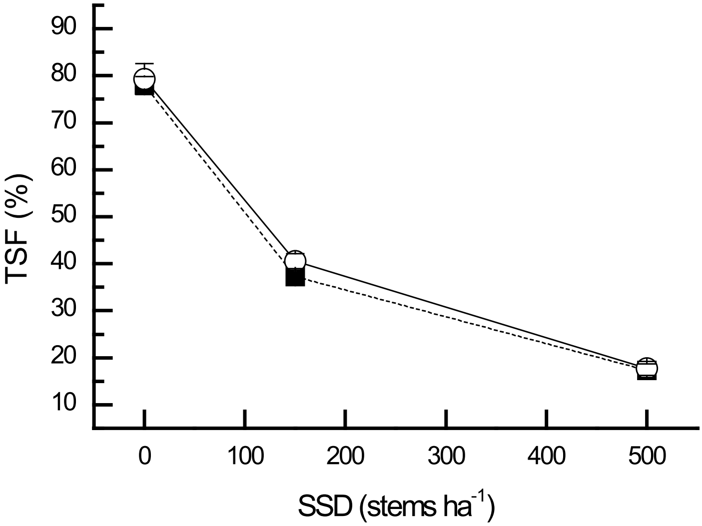

Figure 1. TSF values in SSD 0, SSD 150, and SSD 500 averaged between North and South slopes during growing season 2006 (filled square) and one day in July 2006 (open circle; I). TSF values differed between SSD's at the 0.05 level of significance according to Tukey's multiple comparison test. Error bars denote the standard error of TSF.

Nutrient supply

The response to fertilisation in this work was much less than expected, and the results could be questioned considering dosage and performance. Jarvis and Linder (2000) concluded for example that the effects of temperature on the growth of trees in the boreal forest are mediated by the capture of CO_2 and nutrients much more strongly than by other physiological processes. It should also be considered that soil preparation could make more nutrients available to the seedlings at higher temperatures (as in SSD 0) which can affect growth (Grossnickle, 2000). However, even if it is difficult to fertilise single seedlings optimally in the field, the procedure was supported by knowledge and experience from nurseries in practical forestry (Gulin, pers. comm.) and there was an obvious effect in the clear-cut where it was also very clear that other field vegetation (for example *Luzula pilosa*) gained from the treatment. It thus seems that the poor responses from fertilisation in SSD:s 500 and 150 were not due to inappropriate fertilisation procedures.

The North and South slope were analysed separately since establishment of both direct seeded and planted seedlings differed significantly between the slopes. Differences in light regimes could not directly explain establishment differences as there was no significant difference in transmission values between the slopes. The PPFD-values are for both direct and diffuse radiation and have a resolution of 24 hours, which means that there can still be radiation peaks at different times during a day at the contrasting slopes. There is also a slight difference in site index between the North and South slopes (Table 1; I) with somewhat higher fertility at the South slope .

Emergence

The establishment and growth of seeded seedlings was highly dependent on species and SSD (I). Both *P. abies* and *P. sylvestris* will benefit from increased radiation obtained by canopy gaps (de Chantal*, et al.*, 2003b). On the North slope, the emergence was highest (49.5 seedlings in percent of germinable seeds for and 44.2% for*;* Table 4; I) in SSD 150. On the other hand, on the South slope the conditions in SSD 0 favoured the high emergence of *P. sylvestris* (41.3%;Table 4; I), whereas for *P. abies* there was no significant difference between SSD 0 and SSD 150 (27.8% versus 30.1% respectively;Table 4; I). For *P. abies* on the South slope, the highest values of emergence also tended to be at least 1.5 m away from trees on the north side (ca. 30-35%), whereas the lowest values were between 1 and 2 m on the south side of trees (ca. 20%). The emergence of *P. sylvestris* on the South slope was higher on the north side of trees (31.5%) than on the south side (27.7%) and the emergence 1 m away from trees was lower than the emergence 4 and 6 m away (24.6 %, 33.9%, and 33.4%, respectively; Table 6; I).

The soil preparation method of HuMinMix favoured emergence of seeded seedlings in accordance with previous research (I; Winsa, 1995a). In SSD 150 on the South slope, the emergence of *P. abies* was about 40% higher on HuMinMix (35.1%) than on mineral soil (25.1%; Table 5; I). The emergence of *P. sylvestris* on the North slope was much lower on mineral soil than on HuMinMix in SSD 500 (19.4% and 32.5%, respectively; Table 5; I)), and on the South slope the emergence of *P. sylvestris* was also lower on mineral soil (28.5%) than on HuMin-

Mix (34.8%), irrespectively of SSD. For direct seeded *P. abies*, damage by frost heaving was highest on mineral soil in SSD 0, consistent with Goulet (1995), on the North slope (14.3%) and for *P. sylvestris* frost heaving was highest in SSD 0, irrespectively of soil preparation (15.6; Table 7; I). Predation was lowest in SSD 500 on both slopes (North slope 27.4% and South slope 38.9%; Table 8; I).

Growth and fertilisation effects

Only for *P. abies* on the North slope, fertilised seeded seedlings were significantly taller (ca. 20%) than non-fertilised seedlings in 2004 (I; Figure 2). For planted *P. abies,* fertilised seedlings in SSD 0 were the ones that grew the most (22.2 cm; Table 2; II). Fertilisation had no effect on height growth of planted *P. sylvestris*, but the growth was clearly increasing (from <20 cm to >50 cm) with decreasing SSD. The naturally regenerated seedlings/saplings in the different height classes showed no response in height growth to fertilisation.

Planted seedlings in SSD 0 had the greatest biomass of branches and leading shoot (green biomass; II). On the North slope, fertilisation had an effect on *P. sylvestris* in SSD 0, with fertilised seedlings having a greater green biomass

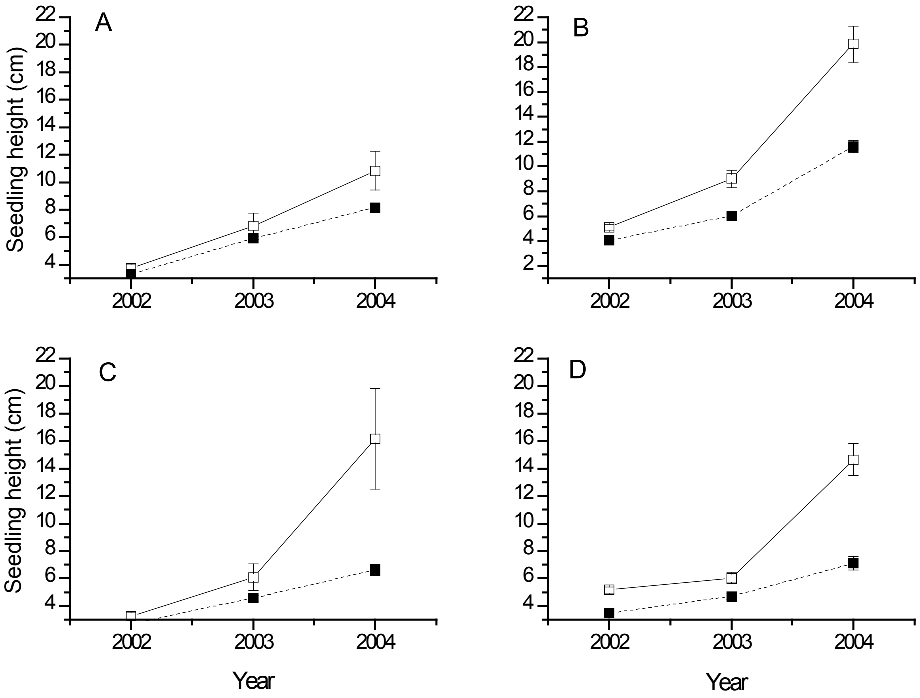

Figure 2. Height of direct seeded seedlings at the end of growing seasons on the North slope, P. abies (A) and P. sylvestris (B) and South slope, P. abies (C) and P. sylvestris (D; I). Open and filled squares are for stand stem density (SSD) 0 and 150, respectively. Error bars denote the standard error of seedling height.

(62.6 g) than non-fertilised seedlings (39.7 g; Table 4; II). In SSD 0 on the South slope, fertilised *P. abies* seedlings had a greater green biomass (40.4 g) than non-fertilised seedlings (23.6 g; Table 4; II). For *P. sylvestris,* seedlings in SSD 500 had the highest fraction of roots (ca. 20%; II). For planted seedlings, comparing the results of dry mass of leading shoot with those of height growth (for the same, non-browsed seedlings) showed differences between species and SSD's (Figure 5; II). With *P. sylvestris* being the more extreme, dry mass of leading shoot in SSD 500 was only 3% of that in SSD 0, while for height growth the corresponding value was almost 30%. Height growth is according to this not a good measurement for overall growth of seedlings, especially not under shelter (i.e. in CCFS's). Inadequate light conditions in SSD 150 and SSD 500, in the stands used for these experiments, made the seedlings in almost all cases incapable of responding to fertilisation. This is in accordance with the result of for example Mitchell (2001) who drew the conclusion that retention of 25% of the preharvest overstorey stand structure can limit the early growth of regenerating montane conifer seedlings presumably as a result of a 47% reduction in available light and not as a result of reduced nutrient availability,

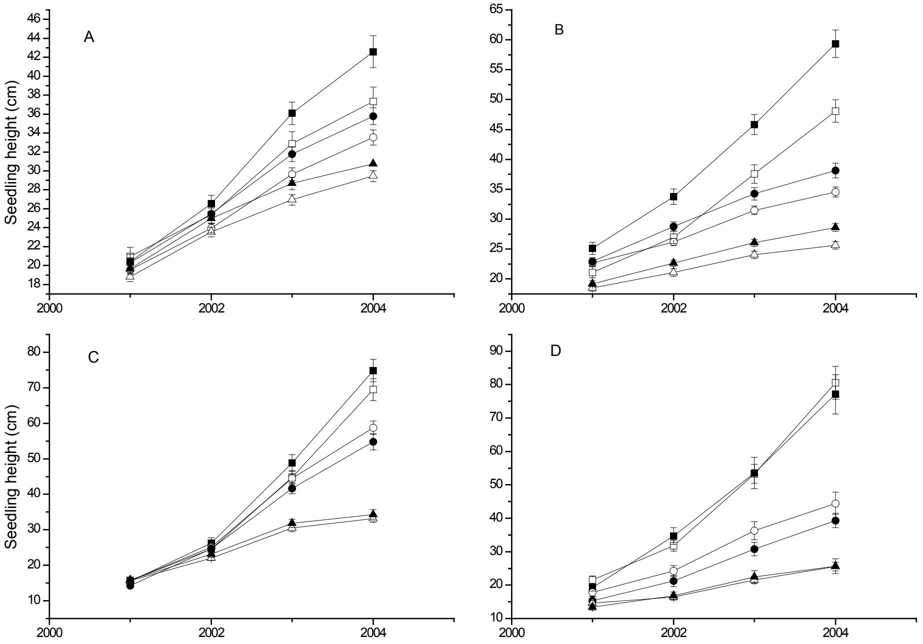

Figure 3. Height of planted seedlings during the years of the experiment for fertilised (filled) and non-fertilised (open) P. abies on the North (A) and South (B) slope, and P. sylvestris on the North (C) and South (D) slope, in stand stem density 0 (squares), 150 (circles), and 500 (triangles; II). Error bars denote the standard error of seedling height.

Regeneration under shelter versus in gaps

The first few years of seedling establishment are critical as seedlings are especially vulnerable to extremes of climate, predation, and pathogens. For the seeded seedlings, *P. abies* on the North Slope was most successful with only 8.8 seedlings in percent of germinable seeds out of 23.8% emerged, after four years (Figure 5; I). The clear patterns that we see for height growth of planted seedlings in relation to SSD, with *P. sylvestris* in SSD 0 having the highest growth, is not surprising considering *P. abies* being shade-tolerant and *P. sylvestris* shade-intolerant (II; Figure 3). Habitat conditions are important and play a major role in determining the success of regeneration and they vary within the forest stand matrix, at gap edges, among gaps, and within gaps. The stand matrix and gap edges have received little study in terms of assessing their suitability for tree establishment and growth (Coates & Burton, 1997). Bergqvist (1999) studied *P. abies* (35-37-year-old at the establishment of the trial) growing under a shelter of *Betula pubescens* Ehrh. and *Betula pendula* Roth. with two different stem densities (300 and 600 stems per ha), and found out that compared to *P. abies* growing on a clear-cut height growth did not differ. Wood volume yield was constantly higher, and diameter growth accelerated initially, on the clear-cut compared to both shelterwood treatments, which did not differ between each other. He concluded that the lack of response in height, together with increased diameter giving decreased slenderness index in the clear-cut, mainly was due to light being the prime limiting factor. Bräker and Baumann (2006) concluded, by examining border trees of several rectangular slots cut for regeneration, that sub-alpine *P. abies* stands 100 years of age, still seem capable of reaction to sudden changes in light availability. The germination, survival and growth of shade-tolerant and shade-intolerant tree species have often been correlated with gap size. Light conditions at ground level throughout forest stands are directly related to gap size, shape, canopy height, and latitude and since light availability can vary sharply over short distances within gaps, position within gap is critically important to the physiology and growth of any individual tree seedling (Wayne & Bazzaz, 1993). Seasonally integrated light transmission at the gap center of a gap of 24 m in diameter in a homogenous birch stand of 10 m in height is about 60%, while at the center of a 12 m gap it is 40% (Comeau *et al*., 1998).

Coates (2000) performed a study on the five conifer species *Thuja plicata*, (western redcedar), *Tsuga heterophylla* (western hemlock), *Abies lasiocarpa* (subalpine fir), hybrid spruce, and *Pinus contorta* (lodgepole pine). The study showed that growth of all species greatly increased from small single-tree gaps to about 1000m^2 gaps, but thereafter little change in growth could be seen up to gaps of 5000m^2. In large and medium gaps (301-1000m^2), the largest trees of all species were found in the middle gap position and there was for most species little difference in growth between the north and south positions. In the smaller gaps, as well as in the forest understorey, total size and growth rates were almost identical for all species.

The silvicultural systems of small group selection (18-m circles) and strip-cutting (18-m strips) in northern latitude forests provide 55% and 68% of total growing season solar radiation, respectively, which allows for penetration of light to the ground surface in sufficient quantities to ensure the development of spruce seedlings (Grossnickle, 2000). One method that has been used in Britain (Mason & Kerr, 2004) is the felling of small groups of 0.1 to 0.5 ha (group shelterwood) and replanting with desired species but taking advantage of natural regeneration when, and if, it appears. A problem with this system in Britain has been rapid vegetation colonisation, but in the northern parts of Scandinavia a system like this would probably give better results as the fertility of stands is usually rather low.

Conclusions and further questions to address

The general conditions of the stand, i.e. most obviously the light environment, seem to matter more than orientation and distance with respect to the nearest tree and the light availability is more important than nutrient supply. Light availability could be used as a predictive management tool, but the response of forest regeneration following silvicultural treatments, such as partial cutting or site preparation, should be linked to estimates of light at ground level (cf. Lieffers *et al.*, 1999). A way to regenerate forests by using the benefits of shelter trees and at the same time creating the desirable conditions of a clear-cut, could be a system where forest gaps are formed within shelterwood. The optimum light and moisture conditions for the species of concern can be met by deciding shelterwood density, gap size, and within gap position. This may give a more secure regeneration, without necessarily reducing regeneration growth, compared to in a clear-cut. Also, shelterwood systems with an orientation of east to west can result in light penetration into the understorey along the south facing cut-face (Grossnickle, 2000). Gap opening sizes need not be very large (0.1 – 0.2 ha minimum) in order for conifer species to achieve growth rates similar to those found in the open conditions of a clear-cut (Coates, 2000). This could possibly be done in a way applicable to conventional forestry, with gap dimensions (e.g. 20-40 × 30-60 m) possible to cut cost-effectively for a conventional harvester working diagonally through a chequered pattern (Figure 4). By seeding or planting there are advantages of not being reliant on natural regeneration and also being able to introduce desired species and genotypes (not always present in the stand). Shade tolerant species could be regenerated in the areas of the gaps with comparably low light levels, while shade-intolerant species would be advantageous to regenerate in the areas with comparably high light levels (Figure 4). In a CCF system species should be chosen depending on stand conditions and degree of cutting, whereas the chosen regeneration method depends for example on the extent of competition by vegetation and risk for predation. The results of this thesis come up with two main questions to consider (Figure 5): (1) how big openings should be created to achieve satisfactory establishment at a certain SSD (light level) in

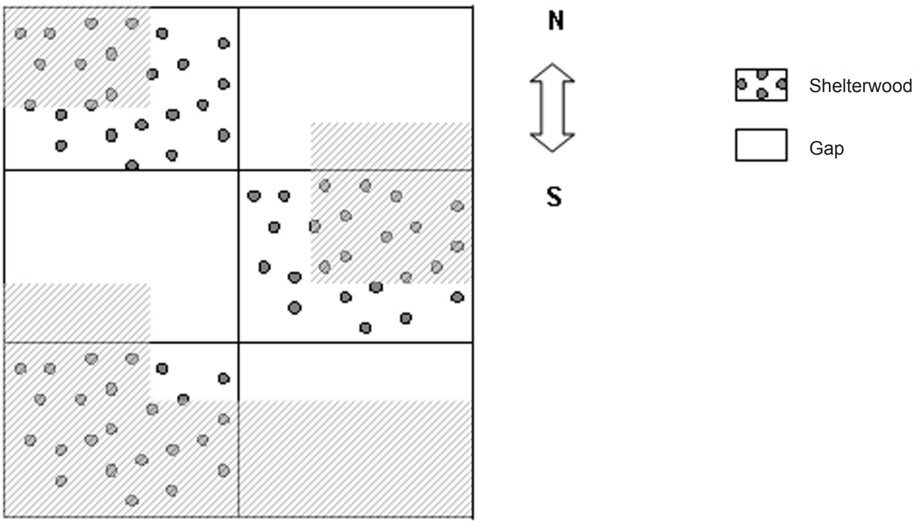

Figure 4. Schematic overview of a chequered gap-shelterwood system in northern latitude forests showing areas with higher and lower (dashed fields) light levels.

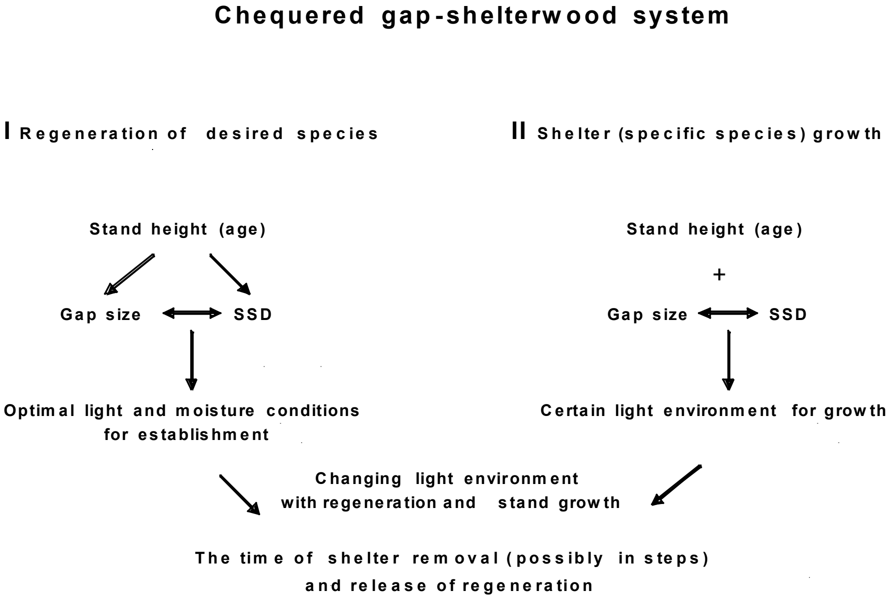

Figure 5. What to consider in order to achieve a chequered gap-shelterwood system for optimal regeneration and growth.

the shelter, and (2) when is the proper time for release of regeneration by cutting the shelterwood? For both *P. abies* and *P. sylvestris*, an increase in radiation by opening the canopy is crucial to maximise growth.

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