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Regeneration Dynamics in Uneven-aged Norway Spruce Forests with Special Emphasis on Single-tree Selection

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Abstract

The thesis summarises results from four separate studies. One study reviews early Swedish regeneration studies (1830-1949) in multi-storied Norway spruce (*Picea abies* (L.) Karst) forests, subjected to single-tree selection and other forms of partial harvests. The review identified shortcomings in the knowledge of regeneration dynamics in multi-storied forests. The other three studies, performed in central and northern Sweden, concern the effects of overstorey density, (expressed as standing volume, basal area and canopy openness), and the effects of ground cover (bilberry [*Vaccinium myrtillus* L.] or herbs [e.g. *Aconitum septentrionale* Koelle]), on regeneration density and height increment. The studies included possible differences between multi-storied and shelterwood stand structure. Furthermore, recruitment, mortality and ingrowth rates were quantified.

Seven years after treatment sapling mean height increment decreased with standing volume in shelterwoods. Results in multi-storied stands were inconsistent. Ten years after harvests, sapling (0.5 m $\leq h <$ 2.0 m) and small tree ($h \geq$ 2.0 m, diameter at breast height < 5 cm) mean height increment increased significantly with canopy openness. Sapling growth showed high correlation with canopy openness, whereas small tree growth showed high correlation with basal area. A multi-storied structure was significantly negative for sapling and small tree height increment. Overstorey standing volume (range 13-333 m^3 ha^{-1}), did not affect seedling ($h <$ 0.5 m) density and height increment, in a virgin forest in northern Sweden, whereas density and height increment of saplings (0.5 m $\leq h \leq$ 1.3 m) decreased significantly with overstorey standing volume. Dominating ground cover did not affect regeneration (0.1 - 1.3 m) density or height increment in the virgin forest. Mortality rates were close to zero. Estimated time to grow through the size interval 0.1 to 1.3 m was 56 years. The recruitment rate into the lowest height class differed little between plots with high and low standing volume. Ingrowth into the tree layer was positively affected by decreasing standing volume.

Keywords: single-tree selection, selection system, shelterwood, virgin forest, advance growth, *Picea abies*, natural regeneration

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Seven years after treatment sapling mean height increment decreased with standing volume in shelterwoods. Results in multi-storied stands were inconsistent. Ten years after harvests, sapling (0.5 m $\leq h < 2.0$ m) and small tree ($h \geq 2.0$ m, diameter at breast height < 5 cm) mean height increment increased significantly with canopy openness. Sapling growth showed high correlation with canopy openness, whereas small tree growth showed high correlation with basal area. A multi-storied structure was significantly negative for sapling and small tree height increment. Overstorey standing volume (range 13-333 m^3 ha^{-1}), did not affect seedling ($h < 0.5$ m) density and height increment, in a virgin forest in northern Sweden, whereas density and height increment of saplings (0.5 m $\leq h \leq 1.3$ m) decreased significantly with overstorey standing volume. Dominating ground cover did not affect regeneration (0.1 - 1.3 m) density or height increment in the virgin forest. Mortality rates were close to zero. Estimated time to grow through the size interval 0.1 to 1.3 m was 56 years. The recruitment rate into the lowest height class differed little between plots with high and low standing volume. Ingrowth into the tree layer was positively affected by decreasing standing volume.

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"Kwistvarfven sitta på grund av den svaga höjdtillväxten tätt intill varandra, och toppskottet är kort och spetsknoppen liten och fin. De nedre grenarna äro däremot ofta långa, hvarigenom den undertryckta telningen ej så sällan får utseende af en något tillspetsad hattsvamp eller ett uppspänt paraply. Den ser ej så synnerligen medtagen ut utan liknar ett hopkrupet rofdjur, som lurar på att vid något lägligt tillfälle gå anfallsvis tillväga"

Lovén 1911

Contents

Appendix

Articles I-IV

The thesis is based on the following articles, which will be referred to by their Roman numerals.

I. Nilson, K. Studies of single-tree selection from 1830-1949 - a review. Manuscript.

II. Nilson, K. & Lundqvist, L. 2001. Effects of stand structure and density on development of natural regeneration in two *Picea abies* stands in Sweden. *Scandinavian Journal of Forest Research 16*, 253-259.

III. Nilson, K. Natural regeneration of Norway spruce (*Picea abies* (L.) Karst) in a virgin forest in northern Sweden. Manuscript.

IV. Chrimes, D. & Nilson, K. Influence of overstorey density on height increment of natural regeneration in a multi-storied *Picea abies* stand in northern Sweden. Manuscript.

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Introduction

Background

The dominance of the clear-cutting system has for long been a cause of concern in relation to its effects on the environment (c.f. Heliövara & Väisänen 1984, Hart 1995, Fries et al. 1997), and in the Swedish Forestry act of 1993 (Anon 1994) environmental aspects and timber values were given equal importance. One way to provide for biodiversity would be to create and maintain multi-storied stands (Liljelund et al. 1992, O'Hara 1996, Helliwell 1997). The "new" management strategies are basically designed to create two or more age (size)-classes, but the resulting stand structures vary, as do the names of the management forms: continuous cover forestry (Yorke 1992, Garfitt 1995), continuous forest (Helliwell 1997), close-to-nature forestry (Mlinsek 1996), near-natural forestry (Benecke 1996), multi-aged forestry (O'Hara 1996), and multicohort forestry (Oliver & Larson 1996). The classical way to create continuous forest cover is single-tree selection (Hart 1995).

In Sweden partial harvests were used during the first decades of the 1900s, a period called "blädningsepoken", the "era of the selection system" (Carbonnier 1978, Mattson & Östlund 1992). Heavy high grading in northern Sweden in the late 1800s had created sparse stands with insufficient regeneration (Holmerz 1877, Örtenbladh 1891). The pulp industry was not yet established in northern Sweden, and with no demand for small dimension timber, the introduction of the clear cutting system was not economically justifiable. The bad economy during the 1930s favoured low cost methods and natural regeneration. This promoted the use and misuse of different forms of irregular shelterwood (Wallmo 1897, Amilon 1930, Petrini 1934) and strip cutting methods (Elgstrand & Rydbeck 1926, Holmgren & Törngren 1932). Early regeneration studies (Holmgren 1914, Nordfors 1928, Tirén 1949) and the national forest survey 1938-48 (Näslund 1948) showed alarming figures of low stand densities and regeneration failure in northern Sweden. In 1950 selection forestry was abandoned in State forests (cf. Carbonnier 1978), and forest companies followed (Andrén 1992). As a consequence there was a break in Swedish selection forestry research until the 1980s. The bad reputation of regeneration failure with selection methods still remains, and in order to challenge the need of alternatives to clear-cutting more knowledge about regeneration dynamics in multi-storied forests is needed.

The selection system

Classification of silvicultural systems and methods has differed over time and between authors. However, most authors acknowledge the distinction between even-aged and uneven-aged forestry (Mattews 1989, Nyland 1996, Smith et al. 1997). The clear cutting system and the selection system are usually seen as each other's opposites, each being the prime example of even-aged and uneven-aged methods, respectively. Between these two extremes there are intermediate methods like strip cutting and group selection, sometimes classified as belonging to even-aged management (e.g. Roach 1974a, Lundqvist 1984, Burschel & Huss 1997), and sometimes to uneven-aged management (e.g. Mattews 1989, Nyland 1996, Smith et al. 1997). The silvicultural system used to maintain uneven-aged stands is usually called the *selection system* and single tree-selection is the classical method within this system (Hart 1995).

Single-tree selection

Single-tree selection requires tree species with the ability to regenerate naturally in a relatively dense stand, survive suppression and slowly increase their growth (Nyland 1996). These qualities are found in shade tolerant tree species (cf. Smith et al. 1997). Single-tree selection is used all over the world with a large number of species, e.g. in Switzerland with beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and Norway spruce (Picea abies (L.) Karst) (Zingg et al. 1997), in USA in southern Arkansas and northern Louisiana with Loblolly pine (*Pinus taeda* L.) (Murphy & Shelton 1994), and in New Hampshire with hardwoods (Leak 1996). The aim is often to prevent erosion or avalanche problems in steep terrain. In Scandinavia, Norway spruce is the tree species most commonly treated with single-tree selection (cf. Lundqvist 1989, Andreassen 1994, Lähde et al. 1999).

In Sweden single-tree selection is used on a small scale in mountain areas, where clear-cutting is not recommended because of risk for regeneration failure due to the harsh climate (Anon 1994). In a forest treated with single-tree selection, the ground should always be covered with trees of all sizes, and standing volume is constantly high (Lundqvist 1989). The area being regenerated is roughly equal to the crown spread of one or two mature trees (Hart 1995). After harvest, the diameter distribution should form an inversely "J-shaped" curve with a decreasing number of stems in each higher diameter class (de Liocourt 1898, Lundqvist 1989, Leak 1996).

Long-term success of single-tree selection requires that trees that die or are removed in harvests are replaced by ingrowth from the seedling layer (Nilsen 1988, Lundqvist 1989, Andreassen 1994). Ingrowth is dependent on three processes: recruitment of new seedlings, and growth and mortality among existing seedlings (Lundqvist 1995, Dobryshev 1999). If ingrowth rates become too low to replace tree mortality or harvest removals, stands will slowly decline, and the multi-layered structure will not be possible to maintain (Lundqvist 1989).

Regeneration in multi-storied spruce forests

Sufficient seedling recruitment is governed by seed supply, seed dispersal, germination, and establishment (Smith et al. 1997). Seed years with a high seed production may occur with 3 to 13 year intervals (Sarvas 1957, Hagner 1965). Far north, and at high altitudes, intervals between seed years can be somewhat longer (Hofgaard 1993b), but viable seeds are produced in low amounts most years (Koski & Tallqvist 1978). Seed dispersal is usually not greater than a few times the height of the seed bearer (Smith et al. 1997). Successful germination depends on having enough moisture (Arnborg 1947, Yli-Vakkuri 1961, Skoklefald 1992, Nyland 1996), and temperature (Mork 1938, Brand 1991). The nature of the spot where the seeds are deposited is also important. Seedlings are often abundant on decomposing logs and stumps (Hofgaard 1993a, Hörnberg et al. 1995), presumably because competitive interaction is moderate (Hörnberg et al. 1995).

Annual height growth is very low for small seedlings in multi-storied spruce forests. Even if it increases as seedlings grow higher (Mitscherlich 1952, Lundqvist 1991), it might take more than 40 years to reach breast height (Nilsen 1988, Lundqvist 1995). There have been doubts about the ability of suppressed understorey trees to increase their height increment after harvest, but Andersson (1988) showed that even old suppressed seedlings can increase their height growth after release. The stagnation period can be very long, i.e. up to 10 years (Skoklefald 1967, Andersson 1988). In shelter woods pre-release seedling size is positively correlated with post-release height growth of advance growth (Skoklefald 1967, Örlander & Karlsson 2000), but a study in multi-storied stands showed that seedling (0.1-2.0 m) mean height is not significant for mean height increment (Lundqvist & Fridman 1996).

Only a few of the seeds that reach the ground germinate and result in established seedlings. The number of one year old Norway spruce seedlings can be up to 40 000 seedlings per hectare (Skoklefald 1967), but annual mortality can be 87-90% initially (Arnborg 1947, Leemans 1991). For seedlings above 10 cm up to 2 m in height, mortality in multi-storied spruce forests drops to less than 10 % per year (Lundqvist 1991). This is similar to what has been observed in shelterwoods (Hagner 1962b, Skoklefald 1967).

There are few studies on growth conditions for natural regeneration in multi-storied Norway spruce stands (c.f. Andreassen 1994), and the effect of overstorey trees on regeneration in shelterwoods (often Scots pine) is much better represented (cf. Örlander & Karlsson 2000). After a partial harvest in a multi-storied stand, moisture and temperature conditions are much more stable compared to the situation after clearcutting. Overstorey removal can increase the risk of drought-related stress in some cases (Tucker & Emmingham 1977). Since moisture is an important factor for seedling germination and establishment (Yli-Vakkuri 1961, Skoklefald 1992), the remaining overstorey can improve regeneration conditions. However, overstorey trees can affect established seedling growth by water and nutrient competition (Hagner 1962b). Spruce regeneration can also suffer from frost damage (Örlander 1993), but in a multi-storied stand overstorey trees decrease the amount of out-going long-wave radiation (Odin et al. 1984). In shelterwoods, von Sydow & Örlander (1994) showed that a remaining overstorey can reduce pine weevil (*Hylobius abietis* L.) damage on seedlings.

In Norway spruce shelterwoods, seedling height increment and density appears to be negatively affected by standing volume (Hagner 1962b, Zybura 1983, Ölander & Karlsson 2000). Studies in multi-storied stands are inconclusive. Some indicate that overstorey density, expressed as standing volume or basal area has negative effects on seedling growth and density (Leemans 1991, Hofgaard 1993a), whereas others indicate no effects (Böhmer 1957, Nilsen 1988, Kolström 1992, Lundqvist & Fridman 1996), or even positive effects (Lundqvist 1991, Sarvas 1944).

Light interception is among the most important factors controlling seedling establishment (Nyland 1996, Oliver & Larson 1996, Smith et al. 1997). Relatively few modern studies exist that give comparisons of light transmission under boreal forests (Messier 1996), and in Sweden studies have been conducted with Scots pine (Ottosson-Löfvenius 1993), silver birch (*Betula pendula* Roth.) (Johansson 1991), and mixed stands of Scots pine and Norway spruce (Johansson 1986). There seems to be a need for studies connecting light availability with seedling growth in boreal multi-storied spruce forests. Many early studies judged openings in single-tree selection forests to be too small for seedling establishment (Barth 1937, Böhmer 1957, Mayer 1960). One possible explanation for the differences between multi-layered and shelterwood Norway spruce regarding the influence of standing volume and basal area on regeneration growth, could be differences in understorey light interception (cf. Messier et al. 1999). Canopy structures can cause differences in amount of transmitted light (Endler 1993), and this may explain the different effects of standing volume and basal area on natural regeneration growth in multi-layered stands and shelterwoods.

Raw humus created by dwarf shrubs has been discussed as a reason for regeneration failure (Hesselman 1916, 1937). Mork (1946) emphasized that bilberry (*Vaccinium myrtillus* L.) can increase the lignin content in the humus, which is unfavourable for regeneration. In the northern Alps Norway spruce natural regeneration is almost non-existent in *Vaccinium*-dominated patches (Pellissier & Trosset 1992). Bilberry litter can inhibit seedling recruitment due to allelopathic effects (Gallet 1993, Pellissier 1994, Jäderlund et al. 1996). On the other hand, Klensmeden (1984) did not find any correlation between thickness of humus layer and seedling density, and a ground cover type with bilberry has also been found to have a favourable effect on spruce regeneration (Schweiger & Sterba 1997). In a recently performed field experiment, removal of bilberry decreased spruce seedling height increment (Chrimes et al., unpublished). Once the seedling is established, surrounding ground cover can influence survival and growth negatively (Arnborg 1943, Nyland 1996). In Sweden, stands with moist and fertile ground conditions have been preferred of old for single-tree selection (Wahlgren 1914, Leijonhufvud 1921, Opsahl 1933, Söderström 1979). Fertile conditions are often indicated by a dense herb layer, which can be an obstacle for spruce regeneration (Hytteborn & Packham 1987, Skoglund & Verwijst 1989). The effect of herbs, indicating fertile soil conditions, and bilberry on spruce regeneration is thus still inconclusive.

Objectives

The main objectives of the thesis were to establish the influence of overstorey density and ground cover, on regeneration density and growth in multi-storied spruce forests, with special emphasis on forests managed with single-tree selection. Overstorey density was expressed as standing volume, canopy openness and basal area, and the studies included possible differences in effects between stands managed with single-tree selection and shelterwoods. Ground cover was expressed as bilberry versus herbs, and recruitment, mortality and ingrowth rates were quantified.

Materials and methods

Study I

Study I is a literature review covering the period 1830-1949 with special emphasis on the methods used in early Swedish regeneration studies conducted in multi-storied stands.

Study II

The field experiment in study II was conducted at two locations: Ätnarova experimental forest south of Gällivare in northern Sweden (67°1' N, 425 m a.s.l.), and north of Östersund in central Sweden (63°24' N, 470 m a.s.l.). At Ätnarova, ground cover was dominated by low herbs (e.g. *Oxalis acetocella* L., *Maiantemum bifolium* (L.) F. W. Schw.) on one half of the plots and by bilberry on the other half (cf. Hägglund & Lundmark 1977). At the southern site, high herbs (e.g. *Geranium silvaticum* L., *Filipendula ulmaria* (L.) Maxim., *Aconitum septentrionale* Koelle) were abundant on all plots. Norway spruce was dominant tree species at both sites, and standing volume ranged between 110 and 190 m^3 ha^{-1} at Ätnarova, and between 240 and 290 m^3 ha^{-1} at Östersund.

In 1990/91 the experiment was established. A two by three factorial design with two replications plus two untreated control plots resulted in fourteen square plots (0.09 ha) at each site. The two factors were overstorey structure (stand thinned from above or below) and density (low, medium or high). When thinning from "*above*", mainly large diameter trees were harvested to maintain a multi-storied structure, and when thinning from "*below*", i.e. harvesting mainly smaller trees, a shelterwood was created. Overstorey density was expressed as standing volume for trees >5 cm dbh. Thinning intensities were 30%, 60% and 85% of standing volume prior to thinning.

In order to avoid that occurrence and growth of regeneration would affect selection of trees to harvest, and to create comparable treatments between sites and replicates, a computer program was used to select trees to be harvested.

In the spring following harvest at each site, five circular 100 m^2 subplots were established in a systematic pattern within each 0.09 ha square. Height and pre-harvest height increment were measured on Norway spruce saplings (0.5 m $\leq h \leq$ 2.0 m) in each subplot and on seedlings (0.1 m $\leq h <$ 0.5 m) within the central 28 m^2 of each circular subplot (also dead seedlings/saplings were recorded). To enable future identification all seedlings and saplings measured were also mapped within the circular subplots. Data on seedling/sapling growth and mortality from seven years after harvest was used in the study. Treatment effects were evaluated using General Linear Model (SPSS, 1999).

Study III

The study was based on data from an inventory performed 1986 on the southwest slope of the Sakkats mountain in the northwest part of the nature reserve Kirjesålandet, lat. 65° 10' N, long. 16° 10' E, 480-600 m a. s. l. in Sweden. The research area, approximately 300 ha, was spruce dominated with approximately 10% of birch (*Betula pubescens* Ehrh). Site index, estimated from site characteristics, ranged from SI 11 to SI 17, which represents a site quality of 1.6 to 2.7 m^3 ha^{-1} year^{-1} (Hägglund & Lundmark 1981). A total of 46 plot centres were systematically aligned over the area, with a distance between plot centres of approximately 150 · 290 m. Norway spruce seedling height (0.1 m-1.3 m) and annual height increment were measured within a 3m radius at each plot (28.3 m^2). Dominant ground cover was recorded according to Hägglund & Lundmark (1977): grass (e.g. *Gymnocarpium dryopteris* (L.) Newm., *Pteridium aquilinum* (L.) Kuhn), bilberry, lingonberry (*Vaccinium vitis-idaea* L.), crowberry (*Empetrum hermafroditum* Hagerup.), or herbs (e.g. *Aconitum septentrionale* Koelle, *Oxalis acetosella* L., *Geranium sylvaticum* L.). All standing Norway spruce and birch trees, both dead and living, with a dbh of at least 5 cm were callipered within a radius of 5.64 m (100 m^2). Height was measured on a total of 26 randomly chosen sample trees, and standing tree volume was then calculated in two steps. First, sample tree volume (V) was calculated, using functions presented by Brandel (1990) for spruce (function no. 100-0), and for birch (function no. 100-01). Then secondary volume functions were calculated, according to Hoffman (1982), and stem volumes were calculated for all trees from their *dbh*. The mean volume of living trees within the 100 m^2 circle plots was 119.5 m^3 ha^{-1}, with a range from 13 to 333 m^3 ha^{-1}. Dead standing trees accounted for 4.5% of the total volume (both living and dead).

The effects of bilberry or herbs on seedling density and height increment were tested with Univariate ANOVA (SPSS, 1999).

According to Lundqvist (1995) seedling recruitment, height growth, and mortality, influence seedling density and ingrowth, to the tree layer. The number of seedlings in a size class at time t is equal to the number of seedlings at a previous time $t-1$, plus recruitment of new seedlings, minus seedlings growing out of the size class, and minus seedlings that have died. By assuming a constant recruitment rate into the lower of two adjacent size classes, and an equal and constant mortality rate for the two classes, the mean annual mortality rate, recruitment rate into the lowest height class and ingrowth into the tree layer were estimated. Estimates for the total seedling population was compared to seedlings on plots with high ($v > 100m^3$) or low ($v < 100m^3$) overstorey density.

Study IV

Study IV was conducted at the Ätnarova experimental forest south of Gällivare in northern Sweden (for details see Study II, northern site). In mid June of 2000 height increment of the last three years were measured on Norway spruce saplings ($0.5 \leq h < 2.0$ m) were measured on the five circular subplots within the 0.09 ha square plots, and on all small trees ($h > 2.0$ m, $dbh < 5.0$ cm). All standing Norway spruce and birch trees ($dbh > 5$ cm) were callipered, and standing volumes were calculated according to Hoffman (1982) and Brandel (1990), as described for study III. Hemispherical photographs were taken at each of the five subplot centres of the fourteen plots, at 0.9 m and 1.9 m from the forest floor to the top of the fish-eye lens, under overcast sky conditions.

The photographs were developed, scanned and cropped using an image-processing program called *Scion Image* (Scion Corp., 1997). Each photograph was cropped to get the exact same total number of pixels within the same field-of-view area. The canopy openness estimates were calculated as the percentage of pixels on each photo with light intensity above a threshold value representing the sky of the total number of pixels in the field-of-view area for each. There were no differences in light availability estimates between the hemispherical photographs taken at 0.90 and 1.9m, and therefore only the photographs at 0.90 m were used.

The data was analysed with step-wise multiple regression (SPSS 1999), with plot mean height increment of saplings and small trees as separate dependent variables, respectively, and canopy openness, stand structure, (i.e., thinned from below or above), combination of canopy openness and stand structure, sapling or small tree mean height plot, and block as independent variables. The procedure was repeated twice, replacing canopy openness with plot basal area and standing volume, respectively. Both stand structure and block variables were used as dummy variables.

Results and discussion

Influence of overstorey density

During the era of the selection system it was believed that one could regenerate the forests with the axe (Wallmo 1897). A lower standing volume with increasing understorey light levels would promote seedling establishment, mineralization of the humus layer, and seed production. This led to unregulated "light cuttings", "regeneration cuttings", and "cleaning cuttings" following the selection harvest. Stands became very sparse and regeneration failed (Näslund 1948). But some early Swedish regeneration studies indicate that only Scots pine seedlings were measured after harvests in Norway spruce dominated stands (Study I). Repeated partial harvests, often based on the diameter distribution, have discredited the selection method before (Hawkins 1962, Seymour 1995).

In study II, seven years after treatment, mean height increment for saplings (0.5 m $\leq h < 2.0$ m) decreased with increasing overstorey standing volume when the stand was thinned from below, at both southern and northern site (Study II, Figs 1 and 2). Earlier studies in shelterwoods have shown concordant results (e.g. Amilon 1929, Hagner 1962a, Zybura 1983). No such relationship was found for saplings on plots thinned from above. The effect of standing volume on seedlings could not be further analysed because of the low seedling density at the southern site. In study III (Fig. 1) seedling ($h < 0.5$ m) density and height increment were unaffected by overstorey standing volume. Lundqvist & Fridman (1996) and Granhus (2001) showed that sapling height increment is unaffected by overstorey basal area. For a small seedling, survival is probably more important than height growth.

The lack of consistent significant results for saplings in study II might be explained by differences in individual microsites after treatment. Studies have shown that microsite is important for plant establishment and early growth (Yli-Vakkuri 1961, Lähde 1978, Jonsson 1999). According to Ydgren (1972) plants react strongly to the environment within a radius of 0.1 m to 0.5 m. It is possible that some of the saplings experienced a positive change of the near-by environment, resulting in an increased height increment, whereas others did not. Another explanation is that regeneration growth reactions were delayed 5 years after treatment, and maybee 7 years was not long enough a time interval.

Ten years after treatment at the northern site, overstorey basal area was significantly negative for both sapling ($0.5 \leq h < 2.0$ m) and small tree ($h \geq 2.0$, $dbh < 5$ cm) growth (Study IV, Tab. 2). This contradicts the hypothesis in study II, where it was assumed that overstorey density would not affect regeneration height increment in a multi-storied stand. The significant effect of structure for growth of both saplings and small trees suggests that basal area and standing volume was more negative in a stand thinned from above compared to a stand thinned from below. A stand thinned from above had a higher overstorey stem density compared to a stand thinned from below at similar basal areas and/or standing volumes (Study IV, Tab.1). For saplings/small trees this might cause a difference in the below-ground competition. Different structures might also cause a difference in light quality (Endler 1993).

In study IV, sapling and small tree mean height increment increased with canopy openness, and this was in accordance with the hypothesis. Canopy openness, and canopy openness and structure, had a high correlation with sapling height increment in study IV (Tab. 2). For small trees, on the other hand, stand basal area and structure had the highest correlation with height increment. This might be explained by the fact that the canopy openness estimates were measured on a lower level than the average height of small trees. However, canopy openness was significant for small trees too, even though the correlation was weak. This indicates that sapling growth was more influenced by light competition (e.g. Weiner 1990, Hara 1992), whereas small trees were more affected by below-ground competition. This conclusion is based on the assumption that canopy openness reflects light availability. Canopy openness is a simplified measure of light in a forest, and describes the diffuse skylight transmission (Chazdon & Foeld 1987). If canopy openness on the other hand is a needle biomass estimate, it reflects root competition. A decrease in basal area and standing volume is reflected in an increase in canopy openness. Therefore, canopy openness might be more of an overstorey density measure, than a light level estimate. Granhus (2001) found that small Norway spruce trees are affected by basal area whereas saplings are not, and concluded that light becomes increasingly important with height. It seems as if the limiting factor for growth might be shifting gradually as the saplings/small trees grow higher, but the exact reasons behind this shift can not be determined based on these results.

Influence by vegetation

In study III, seedling density and height increment were not significantly affected by ground cover with bilberry compared to other ground covers (Study III, Tab. 3). Maybe the presence of bilberry is too simple a measure to give significant results. It could be that bilberry in combination with other factors, for example temperature (cf. Laine & Henttonen 1987), and light availability (cf. Atlegrim & Sjöberg 1996) can give the negative effects described in earlier studies. Regeneration failure in spruce dominated forests was often explained by presence of raw humus created by low shrubs (*Vaccinium* sp.) that had low nitrification rates (Study I). It must be noted that the properties of the humus layer were not measured here. Arnborg (1947) stated that periodic drought in a thick layer (approx. 10 cm) of raw humus was most limiting for regeneration establishment. With a thin humus layer (approx. 5 cm) small seedlings reach the mineral soil earlier, and a short time of drought in the upper part of the humus layer is not limiting. Presence of allelopathic compounds has also been discussed (Gallet 1993, Jäderlund et al. 1996).

In practical silviculture in Sweden natural regeneration of spruce has been recommended on fertile soils with tall herbs (Lundmark 1988), because spruce seedlings (advance growth) are often abundant at such sites. Söderström (1979) stated that fertile site conditions are prerequisites for regeneration in multi-storied spruce forests. In study II, the rich southern site had almost no recruitment of new seedlings (Study II, Fig. 4). The lack of effect from fertile soil conditions could also be seen in that site productivity had little influence on height increment of regeneration in Study II and Study IV. Height increment on control plots was similar between the sites (Study II, Fig 1 and 2), and no difference between the blocks in terms of mean height increment could be found in Study IV. Furthermore, in study III, a ground cover with herbs, indicating fertile soil conditions, did not affect regeneration density or height increment either. The positive effect of fertile soil conditions, indicated by herbs, can be reversed by competition from herbs for light and nutrients (cf. Walter & Breckle 1989, Lieffers & Stadt 1994). The light levels in forests are known to affect the ground vegetation (Stoutjesdijk & Barkman 1992), and thus canopy trees can affect seedlings indirectly through their dominating effect on the properties of understory vegetation (Kuuluvainen et al. 1993).

Recruitment, mortality and ingrowth into the tree layer

Early regeneration studies concentrated on seedling density measured on one occasion a certain number of years after harvest (Study I, Tab. 1). However, seedling density is a product of recruitment, mortality and growth (Lundqvist 1995). Seedlings in a multi-storied forest do not contribute to timber production, until they are about 60-70 years old (Modrzynski 1979, Nilsen 1988, Lundqvist 1995). Therefore, rate of ingrowth into the tree layer is more important than seedling density in studies of regeneration dynamics in multi-storied spruce forests (Study I). Lundqvist (1995) presented estimates for seedling mortality for multi-storied Norway spruce stands in central and southern Sweden, based on the relationship between seedling height and height increment, and more or less constant number of seedlings annually growing into the lowest height class. The annual mortality rates observed in study II were comparable to Lundqvist's estimates.

The large difference in recruitment of new seedlings between sites in study II – low at the rich southern site and high in the north – can be explained by either low establishment rates or high mortality rates among seedlings smaller than 10 cm height. Abundant natural regeneration of spruce along roadsides, on open mineral soil, indicated that lack of seed was probably not the reason. Nor was there reason to believe that the number of microsites suitable for germination, such as decaying logs (cf. Hofgaard 1993a), was lower at the southern site. High mortality rates among germlings and small seedlings thus appear to be the most plausible explanation, possibly caused by the differences in ground vegetation mentioned earlier. Note that the "new" seedlings in study II were probably already established in the mosslayer before the treatments were conducted.

Annual mortality rates were very low in study III compared to study II. As seedlings grow past 10 cm in height, mortality rates are generally about 3 to 10% (cf. Lundqvist 1991). Decreasing recruitment rates during the last decades and/or increasing height increment can explain this, and estimated recruitment rates were in fact lower than ingrowth rates into the tree layer. In other words, seedlings tended to grow through the height classes faster than new seedlings were recruited. Recruitment rates for seedlings under low and high overstorey standing volume, differed little from recruitment rates for the total seedling population. One explanation could be that when overstorey standing volume is low, competition from ground vegetation is higher. It would seem that low recruitment rates into the lowest height class (Study III, Tab 5) would be negative for the ingrowth rate past 1.3 m, and that the stand might be declining. However, northern spruce forests regenerate more during certain seed years, depending on favourable climatic conditions. High seed production has been observed with 3 to 13 year intervals in some studies (Sarvas 1957, Hagner 1965), and in stands far north at high altitudes with somewhat longer intervals (Hofgaard 1993b). Although recruitment of new seedlings might have been low during the last decades, several "seed years" may thus occur during the coming decades. Therefore, one cannot conclude that this forest is degenerating.

The calculations of mortality and ingrowth were based on the assumption that the relationship between seedling height and seedling height increment is more or less constant, and that recruitment into the lowest height class is more or less constant. This is very seldom the case in a natural forest over longer periods (Linder 1998), and is shown by the negative mortality rates, as mentioned above. However, the estimated time to grow through the size interval (56 years) is in accordance with other studies, which have shown that it takes 30-60 years for Norway spruce to reach 1.3 m height (Nilsen 1988, Lundqvist 1995).

Sapling and small tree height increment increased with decreasing overstorey density. One conclusion from this could be to harvest more to increase ingrowth rates, but then one would face the same situation, as during 1920 - 40, with sparse stands and low production per hectare. Heavy cuts can cause severe damage in uneven-aged stands (Spiecker 2001). If only large trees are harvested, the diameter distribution and stocking are not maintained at optimal levels, and this leads to reduced production (Roach 1974b, Nyland 1996, Lähde et al. 2001). One of the prerequisites for the selection system is a continuously high standing volume, and removals should be done often and modestly (Spiecker 2001).

Conclusions

Early studies of the selection system concentrated on seedling density, a certain year after harvest, when judging whether or not it provided sufficient regeneration. However, seedling density is determined by seedling recruitment, growth and mortality, and small seedling recruitment rates and height increment was not much affected by overstorey density in this thesis. Results suggest that saplings ($h \geq 0.5$ m) are better indicators of regeneration performance than small seedlings ($h < 0.5$ m), and that basal area in combination with some variable describing stand structure can give sufficient estimates of ingrowth rates into the tree layer. The structure created when thinning from above, i.e. harvesting mainly large diameter trees, was negative for regeneration growth, and the reasons for this remains unsolved. More research concerning differences in below ground competition and/or light quality between overstorey structures is needed.

Sapling and small tree height increment increased with decreasing overstorey density, but maximizing regeneration height growth is probably not compatible with high sustained yield in an uneven-aged stand.

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