Stand Development and Growth in Uneven-aged Norway Spruce and Multi-layered Scots Pine Forests in Boreal Sweden

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Abstract

The use of the selection system has always been a marginal part of Swedish forestry, and so has research about the system under Swedish conditions. However, the interest in Sweden for uneven-aged forest management has increased because of a rising concern for the ecological and aesthetical consequences from use of the dominating rotation forests system, which creates even-aged forest and has clear-cutting as primary harvesting method.

In this thesis I have studied the possibilities and limitations of the selection system in Swedish boreal forests. Stand development, ingrowth and volume increment has been studied in both Norway spruce (*Picea abies* (L.) H. Karst.), and Scots pine (*Pinus sylvestris* L.) forests.

My studies of uneven-aged Norway spruce show that 1) these forests have the capacity to spontaneously create and maintain an uneven-aged stand structure, 2) there is a positive relation between standing volume and volume increment, and 3) there is no clear relation between the level of ingrowth and stand density.

My studies of multi-layered Scots pine forests show that 1) a multi-layered stand structure is more likely the result of size stratification and not of continuous ingrowth, 2) There is positive relation between standing volume and volume increment, and 3) that a low stand density is seems required for ingrowth to occur on a sustainable level.

The results imply that for boreal Norway spruce forests, a high standing volume would be recommended when the selection system is applied, whereas for boreal Scots pine forest, uneven-aged management should be motivated by other values than stem production, e.g. aesthetical or ecological.

Keywords: Picea abies, Pinus sylvestris, ingrowth, size stratification, selection system, volume increment.

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Tack älskling för ditt tålamod.

Forskning är som lego, det är alltid någon jävla bit som fattas

Martin A. Ahlström

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Ahlström M. A., Lundqvist L. (2015). Stand development during 16-57 years in partially harvested sub-alpine uneven-aged Norway spruce stands reconstructed from increment cores. *Forest Ecology and Management* 350, 81-86.

II Ahlström M. A., Axelsson E. P., Lundqvist L., Mörling T., Valinger E. (2016). Stand development and volume production in multi-layered Scots pine forests in boreal Sweden. *Manuscript.*

III Ahlström M. A., Axelsson E. P., Lundqvist L., Mörling T., Valinger E. (2016). On the scale of competition between trees in a boreal uneven-aged Norway spruce forest in central Sweden. *Manuscript.*

Paper I is reproduced with the permission of the publishers.

The contribution of Martin A. Ahlström to the papers included in this thesis was as follows:

I Analysed the data, performed the calculations and wrote the paper with co-author.

II Planned the experiment together with co-authors, collected the data, analysed the data, performed the calculations and wrote the paper with co-authors.

III Analysed the data, performed the calculations and wrote the paper with co-authors.

1 Introduction

The rotation forest system, creating even-aged forests with clear-cutting as primary harvesting method, is the completely dominating silvicultural system in Sweden, and have been so for more than half a century (Lundmark *et al*. 2013). Concerns have however been raised about the consequences of the extensive use of even-aged forest management, on biodiversity and ecological values in the forest landscape (Niemilä 1997, Bengtsson *et al*. 2000, Matveinen-Huju and Koivula 2008) and voices have been raised by NGOs and scientists for changes in forest management toward an increasing proportion of the forest land managed with uneven-aged silviculture (Kuuluvainen *et al*. 2012, Rudberg 2014).

A general skepticism toward uneven-aged management in the forestry community (Axelsson and Angelstam 2011), partly based on misconceptions and results from historical use of high grading, is one reason for its limited use. Another reason is that the forest area with a tree species composition and stand structure suitable for uneven-aged management is scarce in the Swedish forest landscape (Anon 1992). The marginal use of the selection system and few long-term experiments have led to limited research possibilities and knowledge about uneven-aged forest management in Sweden.

To evaluate and compare different management practices common terminology and definitions are required. The terminology in silviculture can however be both confusing and unclear, not least when it comes to silviculture in multi-aged forests. The confusion is partly a result of differences in European and North American terminology (Troup 1928) but also due to the author's background and education (O'Hara 2002)

For the reader to get some clarity in the terminology a rough scheme was made in which I divided different terms and labels into three different groups; *umbrella terms*, *management philosophies* and *silvicultural systems*. This is not meant as an attempt to create a "final" defined terminology, but rather a terminology in the light of my own background and education.

There are several *umbrella terms* for silvicultural practices that maintains and creates forests with more than one age class. "Uneven-aged silviculture" may be the most traditional one, defined by Helms (1998) as "silviculture creating a forest with three or more age classes”. Some authors would however argue that also the size distribution needs to be taken into account when determining if a forest is uneven-aged or not. Two more comprehensive umbrella term is multi-aged forests, which also includes forests with only two age classes (Helms 1998), and multi-layered forests, defined as forests with two or more distinctive tree canopy layers (Dunster and Dunster 1996) Continuous cover forestry (CCF) is a term frequently found in more recently published literature (e.g. O’Hara 2002, MacDonald *et al*. 2010, Pukkala and Gadow 2012) but it is not clearly defined (Pommerening and Murphy 2004). The most simplified definition of CCF is “silviculture without clear-cutting”, which by this definition includes a wide range of forest structures and treatments.

There are various forms of *management philosophies* that are more or less formalized, some internationally recognizable and some more endemic. Many of these have an ecological focus where forest management practices should mimic natural processes and/or aim to create natural forest structures. Pro Silva and New forestry are two rare examples. (cf. Franklin 1989, O’Hara 1998, Lähde *et al*. 1999, Gamborg and Larsen 2003).

A *silvicultural system* can be described as a plan for management to produce a crop with sustained yield. Troup (1928) defined it as a process by which the crops constituting a forest are tended, removed and replaced by new crops, resulting in the production of stands of distinct form. He further pointed out three central parts of a silvicultural system:

1. The regeneration method.
2. The form of crop produced.
3. The orderly arrangement of the crop.

As for silviculture in general, the classification of silvicultural systems differs between authors and countries (cf. Nyland 1996, Troup 1928). In Swedish forestry mainly two silvicultural systems are recognized; the rotation forest system (even-aged forests) and the selection system (uneven-aged forests) (Albrektson *et al*. 2012).

In the following text both ‘multi-layered’ and ‘uneven-aged’ are used. Multi-layered is defined as two or more distinctive tree canopy layers and uneven-aged as three or more age classes with a decreasing number of stems over diameter.

1.1 The selection system

The selection system is a silvicultural system practiced in forests with uneven-aged stand structure, i.e. with trees in all sizes mixed together within the forest and with a decreasing number of trees over diameter.

The selection system is sometimes divided into two subgroups; single-tree selection system and group selection system (Hawkins 1962, Nyland 1996). In the group selection system, tree-groups are harvested, to create openings of sufficient size to promote regeneration of less shade tolerant species, thus creating small even-aged patches of regeneration (Hawkins 1962). How large the patches can be before being considered as a separate stand and thereby as a clear-cut is however unclear (Hawkins 1962, O'Hara 2014). In the following text the term "selection system" refer to the single-tree selection system.

1.1.1 Stand structure and selection cutting

A classical characteristic for forests managed with selection system (selection forests) is the inversely J-shaped diameter distribution, which Liocourt (1898) was one of the first to describe (Fig. 1).

Figure 1. Principle figure displaying an inversely J-shaped diameter distribution.

The slope of Liocourt’s diameter distribution can be described mathematically by a constant, the q-factor, calculated as the number of trees in a diameter class divided with the number of trees in the next larger class (Schaeffer *et al*. 1930) The number of stems in each diameter class is however also dependent on the class width used, therefore the class width is needed when interpreting the stand structure using the q-factor. Diameter distributions found in uneven-aged forest can also been described with a negative exponential equation (Meyer 1933) and Weibull function (Bailey and Dell 1973).

An inversely J-shaped diameter distribution may be a prerequisite for sustainable selection system management, but it is not an evidence that the forest has been managed with the selection system, or is even suitable for such management. Both the spatial scale (e.g. stand level or landscape level) and time scale (temporal or permanent) need to be considered before any conclusions can be drawn on the basis of the shape of the diameter distribution (Schütz 2002).

The height distribution in a selection forest is often similar to the diameter distribution, with one exception. The height distributions usually have an accumulation of trees in the highest height classes. The reason for this is that height growth among large trees levels off while they continue to grow in diameter (Indermühle 1978).

Selection cutting can be defined as a thinning from above in an uneven-aged forest stand in order to harvest yield and nourish and shape the forest stand (Fischer 1960, Nyland 1996). It is not confined to a certain area of the forest, but instead the cuttings are distributed all over it, in such a manner that an uneven-aged stand structure is maintained (Troup 1928). Selection cutting is sometimes believed to be performed in order to regenerate the stand, but this is not correct and it should not be considered as a regeneration method (Fischer 1960).

1.1.2 Regeneration and ingrowth

Regeneration in selection forests is not limited to a certain “regeneration phase”, nor to a certain spatial area, and no specific regeneration operations are conducted. Instead regeneration is continuous over time, and distributed over the whole forest area (Troup 1928).

Trees that are harvested and lost through mortality must eventually be replaced by ingrowth. The survival and growth of established seedlings and saplings are therefore crucial for long term sustainability of the system (Lundqvist 1995). Growth among seedlings and saplings in boreal uneven-aged forests is very slow (Saksa and Valkonen 2011) and it often takes 35-60 years, or even up to 100 years, for a seedling to reach 1.3 m in height (Lundqvist 1993, Eerikäinen *et al*.

2014). Therefore, trees that are about to be harvested a 100 years from now, need to be present in the stand today.

1.1.3 Growth and yield

From the experiments done in Fennoscandia, the general conclusion is that there is a positive relation between standing volume and volume increment in uneven-aged Norway spruce forests, such that the volume increment increases over standing volume to a certain level of stand density, whereafter it becomes more or less constant (Näslund 1942, Böhmer 1957, Andreassen 1994, Lundqvist 1994). Such a relation between stand density and growth has also been reported from other parts of the world and with other tree species (Murphy and Shelton 1994, Groot 2002, Lohmander and Limaei 2008). To sustain a high sustainable production it is, therefore, important that the residual stand density after each harvest operation is kept on an acceptably high level.

1.1.4 Tree species

In the selection system seedlings, saplings, and small trees need to have the capability to survive and grow under the canopy of larger trees in order to supply a sufficient ingrowth (Hawkins 1962). Therefore, shade tolerant species are required for sustainable selection system management with high long-term growth and yield.

However, there are several examples were shade-intolerant species are managed with selection cuttings, and display more or less uneven-aged stand structures (Loewenstein et al 2000, Shelton and Cain 2000, Orois and Soalleiro 2002). Success with selection management in forests consisting of shade-intolerant species, or a mix of shade-intolerant and shade-tolerant species, requires that the stand density is reduced to a level were regeneration and ingrowth can occur (O’Hara 1998). This requires a compromise between a stand density maximized for growth and yield, and conditions for sufficient regeneration and ingrowth (Oliver and Larson 1996, Shelton and Cain 2000, Schütz 2002). A potential problem with selection management in forests consisting of shade-intolerant species is invasion and increasing dominance of shade-tolerant species (O’Hara 1998, Shelton and Cain 2000, Liang et al 2005). This is a problem that can be both costly and time consuming to avoid (O’Hara 1998).

1.2 The history of regulated forestry and the selection system in Sweden

Dominating management practice in Swedish forestry was for centuries a kind of selective cuttings, with farmers extracting fire wood, timber and wood for house hold needs (Arpi 1959, Kardell 2004, Enander 2007), with little concern about reforestation and future yield.

The first regulated silvicultural system to be introduced was the rotation forest system. It began in the southern and central parts of Sweden, and did not become more widely used until the middle of the 19th century, and then mainly in state and corporate owned forests (Wahlgren and Schotte 1928; Kardell 2004). Swedish forest research was in limited until the beginning of the 20th century, and knowledge about forest management was to large extent obtained from Germany or by German foresters that came to the Sweden (Arpi 1959; Enander 2007).

At the end of the 19th century, influences from Germany resulted in criticism against the rotation forest system in Sweden, and instead a new form of forestry, with a more liberal cutting regime, was advocated. The new, preferred form of forest management was the selection system, which had begun to be defined and regulated by forest scientists in central Europe. A factor that contributed to the interest in Sweden for this new management practice was the forest regeneration law implemented in 1903. Profitability was low during the economic crisis in 1920-1930, and by using selection cuttings, costs for artificial regeneration could be avoided (Enander 2007).

However, the new silvicultural system, the selection system, was never really used or even fully understood in Sweden. Partial harvests, usually called selection management, were carried out in all types of stands, irrespective of initial stand structure or tree species (Arpi 1959, Enanader 2007). In reality, much of the harvests were simply exploitive cuttings and not what we today would characterize as a regulated silvicultural system.

In most of northern and parts of central Sweden the use of the rotation forest system had been very limited during the 19th century. Instead the prevailing management practice had been diameter limit cuttings, providing timber for the expanding saw mill industry (Arpi 1959). The lack of tradition in using the rotation forest system made it easy to implement the new ‘selective’ management practice. After all, the difference between the prevailing diameter limit cuttings and the new ‘selective’ partial cuttings were small (Arpi 1959).

With the expansion of the pulp industry, which made also smaller trees economically valuable, forests which had previously been subjected to diameter limit harvests were now once again partially cut, resulting in depleted (Fig. 2), and sometimes almost cleaned forest stands (Enander 2007).

Figure 2. Depleted stand after partial harvest around 1900. Photo: Holmgren, A.

In the 1930s the opinion in the forest community once again turned towards the rotation forest system. The lack of regeneration, and the low yield in the partially cut (exploited) forests, raised concern among foresters and land-owners (Arpi 1959). From the middle of the 20th century, the use of the rotation forest system increased rapidly, starting on corporate- and state-owned forest land, but soon also on private forest land (Arpi 1959). The rapid shift in management practices towards the rotation forest system were partly a result of the mechanization that started after the Second World War.

In conclusion the selection system, as the regulated and defined silvicultural system as we know it today, has only been used to a very limited extent in Sweden, and mainly by private land owners.

1.3 Objectives

To meet a growing concern about ecological and recreational values in the forest landscape, and with an increasing interest in uneven-aged forest management, more knowledge is needed about the possibilities and the limitations of the selection system.
The main purpose of this thesis has been to study stand structure dynamics, competition, and productivity in uneven-aged Norway spruce forests and in multi-layered Scots pine forests in boreal Sweden.

The objectives have been to evaluate:

- If boreal uneven-aged Norway spruce forests have the capacity to spontaneously restore their stem density and restore/strive toward an uneven-aged stand structure after being heavily partially harvested (**Paper I, Paper III**).

- If a positive relation between standing volume and volume increment can be found in uneven-aged Norway spruce and multi-layered Scots pine forests (**Paper I**, **Paper II**).

- If a reduction in stand density is required in multi-layered Scots pine forests for abundant regeneration and subsequent ingrowth (**Paper II**).

- If a multi-layered stand structure in Scots pine forests is a result from continuous regeneration and ingrowth, or size stratification within even-aged cohorts (**Paper II**).

- If individual tree growth in boreal uneven-aged Norway spruce forests is proportional to size, indicating a symmetric competition. (**Paper III**).

- If individual tree growth in uneven-aged Norway spruce forest is significantly correlated with the surrounding basal area in the vicinity of the tree (within a radius of 5 m), and the correlation decreases with increasing radius (10 and 15 m) (**Paper III**).

2 Materials and methods

2.1 Paper I

Seven partially harvested stands were included in the study, all of them situated in northern Sweden in the county of Västerbotten. Four stands were located at Granliden (Lat. 64,8° N, Long. 16,0° E) and three stands at Eriksberg (Lat. 65,0° N, Long. 15,8° E), altitudes ranging between 400 and 540 m a.s.l. The time since last harvest varied among the stands, from 16 to 57 years before inventory. Norway spruce (*Picea abies* (L.) H. Karst.) was the dominating tree species (> 90 % of total standing volume), with small additions of deciduous tree species. The soils were moraine, the soil moisture was mesic, and the site productivity 2.3-3.6 m^3 ha^{-1} yr^{-1}, estimated according to Hägglund and Lundmark (1981).

Two circular plots (each with an area of 1000 m^2) were inventoried in each stand. All trees with dbh (diameter at breast height, 1.3 m above ground) $\geq$ 5 cm, and all stumps deemed to originate from the last harvest, were calipered approximately 0.3 m above ground. On each circular plot, 2-4 sample trees were randomly chosen in each 2 cm diameter class, measured for height and had an increment core taken at breast height. For sample trees of Norway spruce height to first live branch, stump diameter and bark thickness were also measured. The inventories were carried out in the autumns of 1993 and 1994.

Pre-harvest and historical stem density and stand structure were reconstructed from the increment cores (for more details about the reconstruction procedure see section 2.4). Ingrowth was calculated as the difference in number of stems between reconstructed years. Stem volume over bark was calculated with primary equations developed by Brandel (1990), using reconstructed stem diameter and the diameter-height relations generated from the sample trees. Secondary volume equations were then calculated for each stand with linear regression.

2.2 Paper II

Four Scots pine (*Pinus sylvestris* L.) dominated stands, two northern (Fig. 3) (Lat. 64° N) and two southern (Fig. 4) (Lat. 60° N) were included in the study. The stands were subjectively selected with the prerequisites that the stands appeared to have a multi-layered stand structure and that past management was known and recorded. Scots pine represented more than 90 % of the standing volume in all stands, with an addition of scattered Norway spruce (*Picea abies* (L.) H. Karst.) and birch (*Betula pubescens* Ehrh and *Betula pendula* Roth). The site productivity, estimated from site characteristics according to Hägglund and Lundmark (1981), was 3.7 m^3 ha^{-1} yr^{-1} in the northern stands, and 5.5 m^3 ha^{-1} yr^{-1} and 4.7 m^3 ha^{-1} yr^{-1}, respectively, in the two southern stands.

All measurements were done in the autumn of 2013. Two circular primary plots (each with an area of 1256 m^2) were deployed in each stand, and in the centre of each primary plot a secondary circular plot (area of 314 m^2) was established. Within the primary plots all trees with dbh $\geq$ 4 cm were numbered and calipered. Total tree height, bark thickness and height to the first live branch were measured on 1-3 sample trees of Scots pine and Norway spruce respectively in each 2 cm diameter class. An increment core was also taken at breast height from each sample tree.

In the secondary plots all coniferous (Scots pine and Norway spruce) saplings were recorded, and total height and the length of the last leading shoot (leader) was measured. For Scots pine saplings also total length of the last 5, 10 and 15 leaders were measured, and age was estimated by counting whorls.

Saplings were defined as trees > 0.5 m in height and < 4 cm dbh.

Historical diameter and age distributions were reconstructed from the increment cores, 25 and 50 years back from the year of inventory (for more details about the reconstruction procedure see section 2.4). Ingrowth of trees and saplings was calculated as the net difference in number of trees/saplings between each reconstructed year. Stem volume over bark was calculated with primary equations developed by Brandel (1990), using reconstructed stem diameter and the diameter-height relations generated from the sample trees. Secondary stem volume equations were then calculated for each stand.

Figure 3. Stand N1 (above) and stand N2 (below). Photo: Martin A. Ahlström.

Figure 4. Stand S1 (above) and stand S2 (below). Photo: Erik Valinger.

2.3 Paper III

The experimental site was located in the central part of Sweden (63.39 Lat., 15.14 Long.) approximately 35 km north-east of Östersund at an altitude of 475 m a.s.l. with Norway spruce (*Picea abies* (L.) H. Karst.) as the dominating tree species (>95 % of total standing volume). The stand structure was uneven-aged, displaying an inversely J-shaped diameter distribution. Standing volume ranged between 200 and 300 m^3 ha^{-1}. Soil moisture was mesic and site productivity was 5.5 ha^{-1} yr^{-1}, estimated from site characteristics according to Hägglund and Lundmark (1981).

The experiment consisted of 8 quadratic primary plots, with a size of 0.25 ha, which were all measured before treatment. All trees with dbh >5 cm were calipered, and mapped (X, Y coordinates). Sample trees were measured for height. Treatments were thinning from above with three different thinning intensities, High (H), medium (M), low (L), and an untreated control (C), replicated in two blocks. Removed basal area was approximately 85 % in treatment H, 65 % in M, and 45 % in L.

All thinned plots were re-calipered after treatment and also re-measured in 2001, 2006 and 2011, in which also sample trees were measured for height, and new trees that reached a dbh > 5cm were mapped and calipered.

Competition intensity was estimated with two different indices: surrounding basal area and surrounding number of neighbouring trees. The competition intensity was calculated for each focal tree using three different radii for the circular competition zones: 5, 10 and 15 m around the focal tree.

Focal trees were all located within a quadratic 15×15 m area in the center of each primary plot, thus having more than 15 m from the focal tree to the edge of the primary plot.

The focal trees were divided into two groups, small trees (dbh ≤17.6 cm) and large trees (dbh >17.6 cm).

A linear regression model was used to evaluate the relation between individual tree growth and competition intensity. Linear regression was also used to evaluate the relation between individual tree growth and tree size. Tree mortality was calculated from 1991 to 2011 in treatment C and from 2001 to 2011 in treatment L, M, and H. The shorter period (2001-2011) for thinned plots were chosen to avoid mortality caused by harvest induced damage after treatment.

2.4 Stand reconstruction

A challenge for many forest researchers studying stand development, is the long time span between establishment and evaluation of the result of a field experiment. Stand reconstruction is a potential solution to that problem. By taking increment cores from a sufficient number of trees and measure the annual ring width, it is possible to reconstruct historical stand structures and estimate ingrowth and volume increment.

2.4.1 Data analysis and calculations

Before the increment cores were analysed, linear bark equations were calculated to be used when reconstructing historical diameters over bark. Data (dbh and bark thickness) from sample trees were used to calculate bark equations for Scots pine and Norway spruce, whereas double bark thickness for birch was calculated as $^1/_{10}$ of the dbh.

Increment cores collected in the field were soaked in water for at least one hour before further analyses in the laboratory. This was done so that the increment cores would resume their original size after being dried during transportation and storage (cf. Eklund 1951). After swelling, the increment cores were planed and the ring widths measured in a WinDendro scanner (Regent instruments, Quebec, Canada) with a precision of 0.1 mm.

The increment cores were pooled for each stand (Paper I) or treatment (Paper II) and for each 2 cm diameter class. The average ring width of the sample trees for each 2 cm diameter class and year were then calculated and used as the average for all trees in the same diameter class.

Historical diameters over bark were constructed as:

$$d_t = d - 2(\sum_{i=1}^{t} wi/(1-c))$$

Where d is dbh, t is the number of years before the evaluation, wi is the calculated average annual ring widths, and c is the regression coefficient for the linear bark thickness equation.

2.4.2 Stand reconstruction and tree mortality

The stand reconstruction method also has a disadvantage, which need to be considered. When reconstructing a stand backward in time, only trees that is alive at the time when the increments cores were taken are included (Lundqvist 2004). Trees that have died during the reconstruction period can in most cases not be accounted for, leading to an underestimation of the historical number of trees and standing volume. By underestimating the historical standing volume the average volume increment for the whole reconstruction periods become overestimated. This is to some extent compensated by the volume growth of trees that died, since they also contributed to the total volume production while they were alive.

The size of the estimation error when doing stand reconstructions is increasing with increasing mortality during the reconstructed period, which in most cases are correlated with the length of the reconstruction period. The length of the reconstruction period must therefore be adjusted to the mortality rate in the specific forest, if tree mortality has been substantial. If the reconstruction period is very long, records of mortality is required to get reliable results.

3 Results and discussion

3.1 Norway spruce (Paper I and III)

3.1.1 Stand structure development

All partially harvested stands (Paper I) displayed diameter distributions that better resembled an inverted J at the time of the final inventory, than directly after harvest (Fig. 5). The uneven-aged diameter distributions (Paper III) in the untreated control plots (C) were maintained and thinned plots (H, M, and L) developed towards increased size heterogeneity during the observation period (Fig. 6, 7).

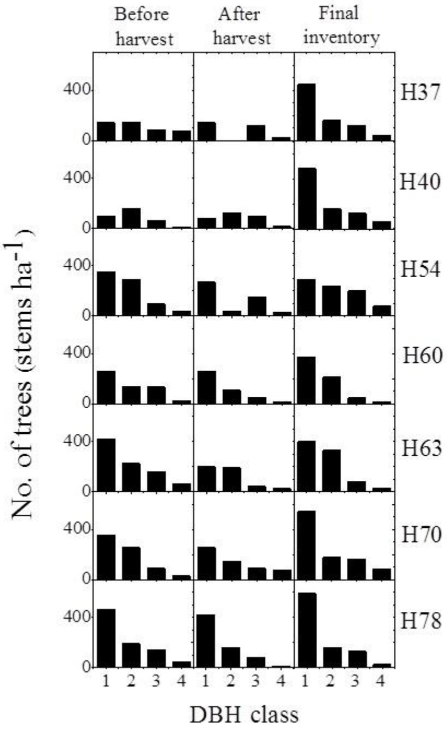

Figure 5. Diameter distribution (Paper I) before (left), after (center) and at the final inventory (right) for each stand. Number 1-4 on the x-axis represent diameter classes D1-D4 which each represent ¼ of the diameter range from 5 cm to the current maximum dbh in the stand.

These results were in line with Lundqvist (2004) who reported sub-alpine Norway spruce stands to be striving towards increased size heterogeneity after partial harvests. Spontaneously created uneven-aged stand structures have also been reported from studies in virgin Norway spruce forests (Hytteborn *et al*. 1987, Hofgaard 1993, Linder *et al*. 1997, Svensson and Jeglum 2001) and in old-growth Norway spruce swamp forests (Hörnber *et al*. 1995).

This indicates that boreal Norway spruce forests, at low and medium fertile sites, can both maintain and restore an uneven-aged stand structure after being heavily partially harvested.

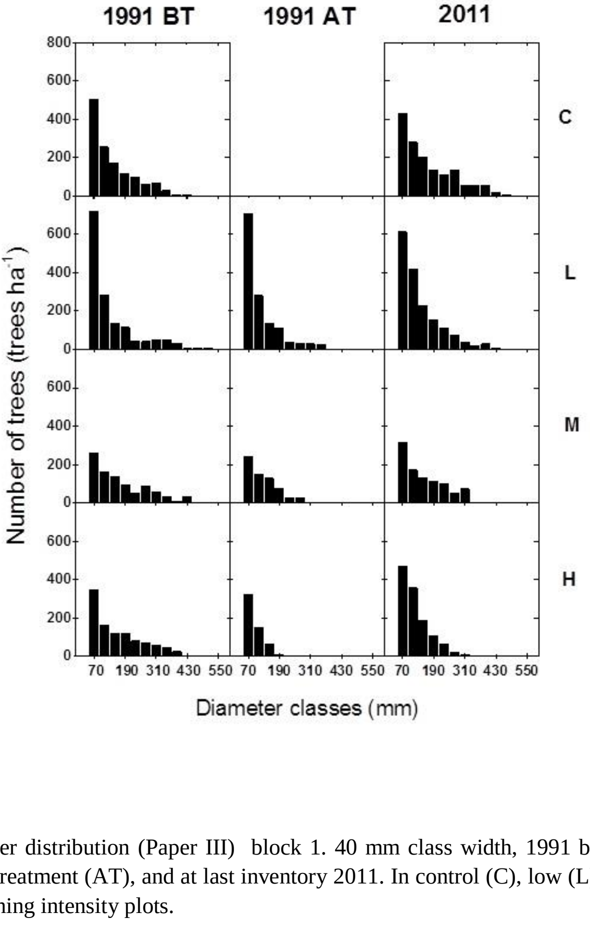

Figure 6. Diameter distribution (Paper III) block 1. 40 mm class width, 1991 before treatment (BT), 1991 after treatment (AT), and at last inventory 2011. In control (C), low (L), medium (M), and high (H) thinning intensity plots.

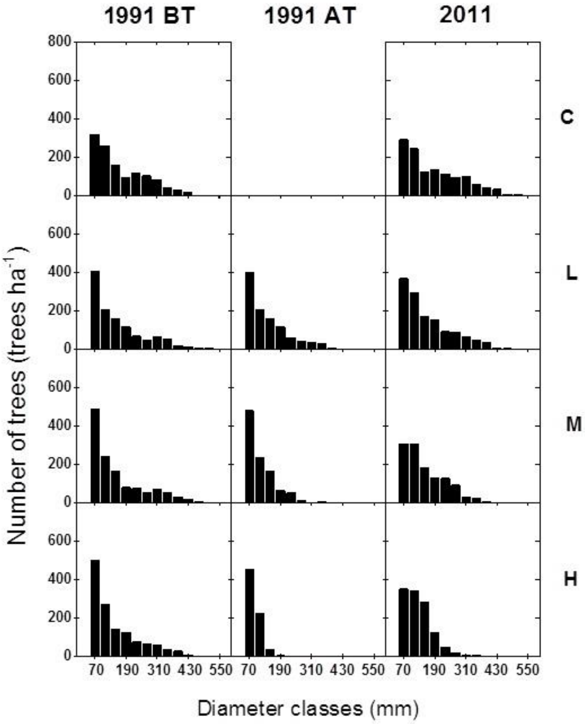

Figure 7. Diameter distribution block 2 (Paper III). For more details see figure 6.

3.1.2 Growth and yield

The positive relation (Paper I) between standing volume and volume increment in six out of seven stands (Fig. 8), was in line with several other studies in uneven-aged Norway spruce forests under boreal conditions e.g. Andreassen 1994, Lundqvist 1994 and Lähde *et al*. 2002. That thinning in general decreases the total production in a stand have also been pointed out by e.g. Smith (1986).

However, our results differ from Lundqvist's (2004) who found no clear relation between standing volume and volume increment in eight uneven-aged Norway spruce stands subjected to partial harvests. The lack of relationship in Lundqvist's study could possibly be explained by the intensive thinning regimes in the past and by resulting small residual standing volumes (9-34 m^3 ha^{-1}) in the beginning of the study period. With such low standing volumes and volume increments, a relation between them may not be possible to find.

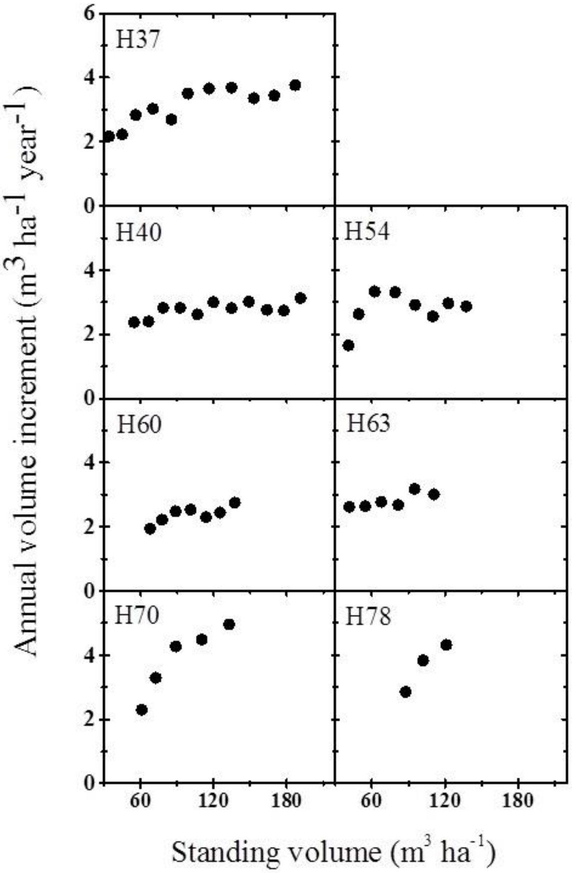

Figure 8. Average annual volume increment in studied stands during each reconstructed five year period vs. standing volume at the beginning of each five year period.

3.1.3 Competition

We found a significant ($p < 0.05$) positive relationship between tree size and individual tree growth for small trees (dbh <17.6 cm) whereas no such correlation were found among large trees (dbh ≥17.6 cm) with the exception for trees in treatment C (Paper III), (Fig. 9, 10).

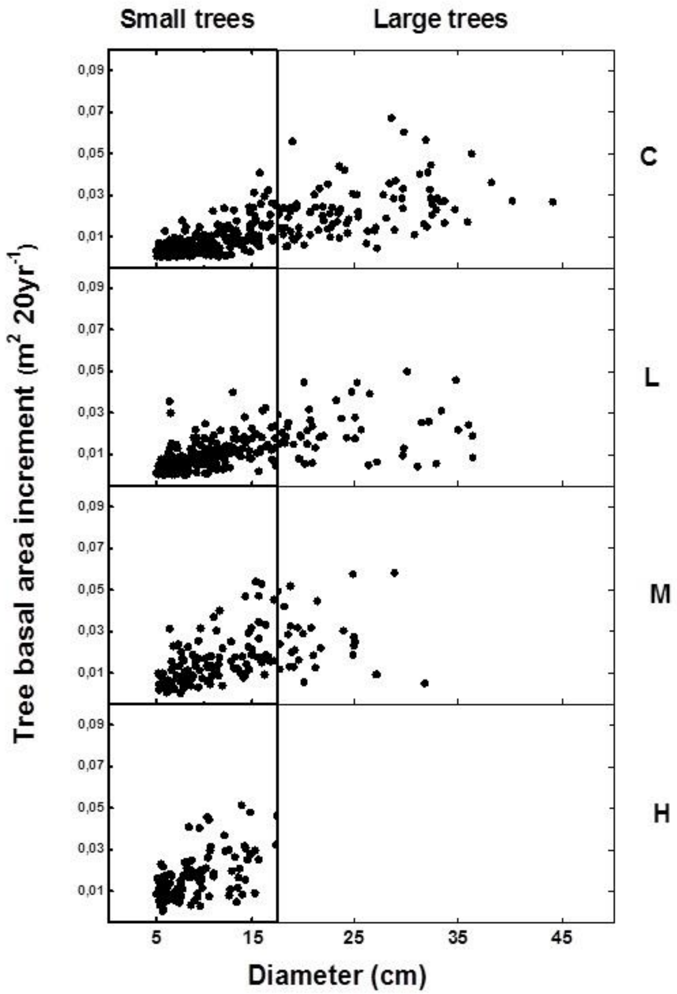

Figure 9. Relation between dbh and tree basal area increment 1991-2011 in **block 1**.

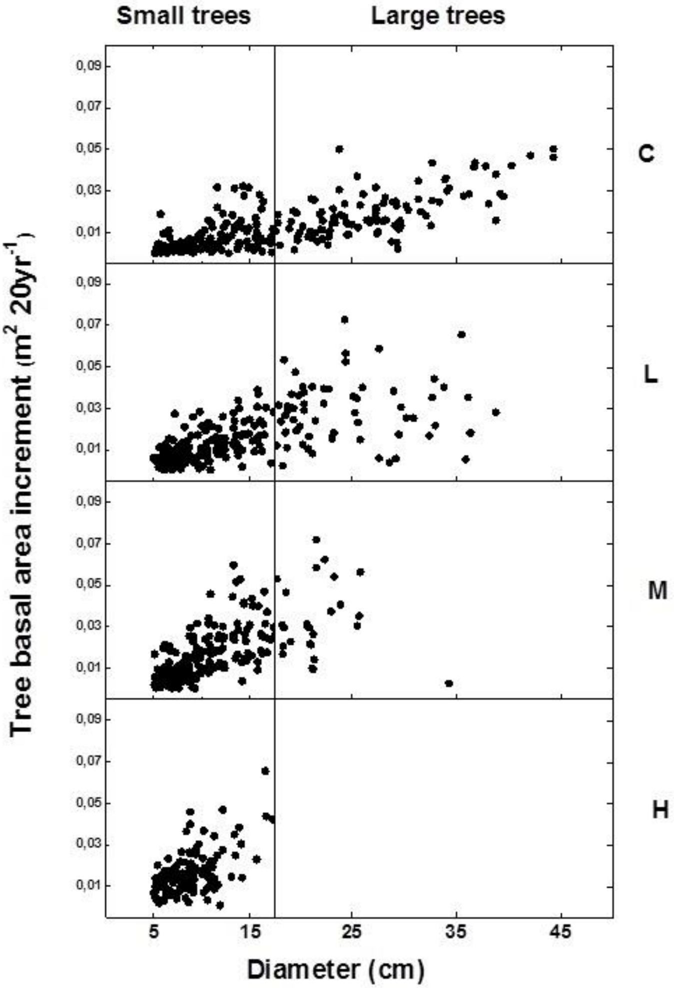

Figure 10. Relation between dbh and tree basal area increment 1991-2011 in **block 2**.

These results were generally in line with what Weiner (1990) hypothesized about competition for belowground resources (symmetric competition) with increasing growth over size among small trees and constant growth over size among larger trees. If growth instead would be limited by light, leading to asymmetric competition, we should have expected to see a size-growth relationship with a threshold size for additional growth, or an exponential-shaped growth over all size classes, according to Weiner (1990).

The conclusion that the available amount of below ground resources in our study were the limiting growth factor corresponded with Tamm's (1991) statement that growth in boreal forest are mainly limited by the available amount of nitrogen. Similar results have also been reported by Lundqvist (1994) who reported size symmetric competition in a boreal uneven-aged Norway spruce forest in northern Sweden.

Individual tree growth in treatment C did, however, deviate from the other treatments in our study and from what Weiner (1990) hypothesised, by displaying an increasing growth over size over the whole tree size spectrum. Treatment C, block 2 (C2) had the highest stand density in our study and also the plot that most clearly displayed a size-growth relationship with increasing growth over size without tendency to level off. Schwinning and Weiner (1998) suggested that competition symmetry in a population is a continuum with a changing degree of symmetric and asymmetric competition as the resource availability for above- and below-ground resources are changing. A possible explanation for the size-growth relationship seen in C2 and to some extent in C1, could thereby be that competition on these plots start to shift from symmetric- to asymmetric competition as light becomes a limitation for small and medium sized trees when the stand density increases (cf. Weiner and Thomas 1986).

The variable (Paper III) that best explained individual tree growth among small trees was tree size, which was significantly correlated with growth in all combinations of treatments and competition zones except for treatment H, radius 5 m. Tree size was weaker as a predictor for individual tree growth among large trees, except for treatment C in which significant correlations were found.

No significant correlation were found between individual tree growth and stem density. Significant correlation between individual tree growth and surrounding basal area was only found in two treatments (C and M) within a radius of 15 m, and only among small trees.

3.1.4 Ingrowth

The mean ingrowth (Paper I) past 5.0 cm dbh were 13.3 stems ha^{-1} yr^{-1}, varying from 7.9 to 23.0 stems ha^{-1} yr^{-1} between stands. This was on the same level as 3-33 stems ha^{-1} yr^{-1} past 8.5 cm dbh and 5-17 above ha^{-1} yr^{-1} past 5 cm dbh reported from comparable studies in boreal uneven-aged Norway spruce forests (Lundqvist (1993, 2004).

The positive relation between ingrowth and stand density that could be perceived in several stands was most likely an artefact and not a true relationship. Norway spruce saplings under the ingrowth threshold increased their growth when the stand density was decreased (Chrimes and Nilson 2005) by harvest, creating a “flush” of ingrowth (Lundqvist 1995). This conclusion was supported by the lack of such a relation in the earliest harvested stands, i.e. stands H37, H40, and H54. In these stands, the ingrowth “flush” had already passed and the accuracy with which the stand development could be reconstructed was not high enough to catch a “flush” of ingrowth so far back in time.

The conclusion that no correlation was present between ingrowth and standing volume was in line with earlier studies in uneven-aged Norway spruce forests in Sweden (Lundqvist 1993, Lundqvist 2004). This result may be found rather strange since studies have shown that the height growth among Norway spruce seedlings/saplings increases with decreasing stand density in uneven-aged forests (Golser and Hasenauer 1997, Chrimes and Nilson 2005, Eerikäinen et al 2014), which thereby would increase ingrowth. This assumption that ingrowth should increase seems indeed to be correct on basis of our results and simulations by Lundqvist (1995). The long-term ingrowth level was however not only a result of seedling/sapling height growth, but also of establishment rate of seedlings, and the mortality rate among seedlings/saplings under the ingrowth threshold (Lundqvist 1995). Reported results on the effect of stand density on both seedling establishment (Lundqvist 1991, Hofgaard 1993, Lundqvist and Fridman 1996, Saksa and Valkonen 2011) and seedling/sapling mortality (Lundqvist and Fridman 1996, Nilson and Lundqvist 2001) have been inconclusive. Instead other factors such as the amount of seed crops (Saksa and Valkonen 2011), the seedbed properties (Valkonen and Maguire 2005) and climate conditions (Kullman 1986) seems to have greater effect on seedling establishment. Also unfavourable weather conditions, abundance of damaging agents, and exposure to frost (Hofgaard 1993, Örlander and Karlsson 2000) seems to affect the mortality rate among seedlings/saplings more than stand density does. Harvest intensity and operating system during selection cutting is also a factor that have to be taken into consideration in terms of seedling/sapling mortality (Fjeld and Granhus 1998, Surakka et al. 2011). The combination of all factors effecting seedling/sapling growth, establishment and mortality makes long-term ingrowth a complex process, in which stand density only constitutes as one factor.

3.2 Scots pine (Paper II)

3.2.1 Stand structure and ingrowth

In 2013 all stands had diameter distributions that were more heterogeneous compared to the beginning of the reconstruction period in 1963 (Fig. 11). At the time both stand N2 and S2 had a majority of the trees in the two lowest diameter classes and S1 had most trees in the diameter class 30-40 cm. Only stand N1 had a diameter distribution in 1963 with a relatively even distribution of trees over size classes.

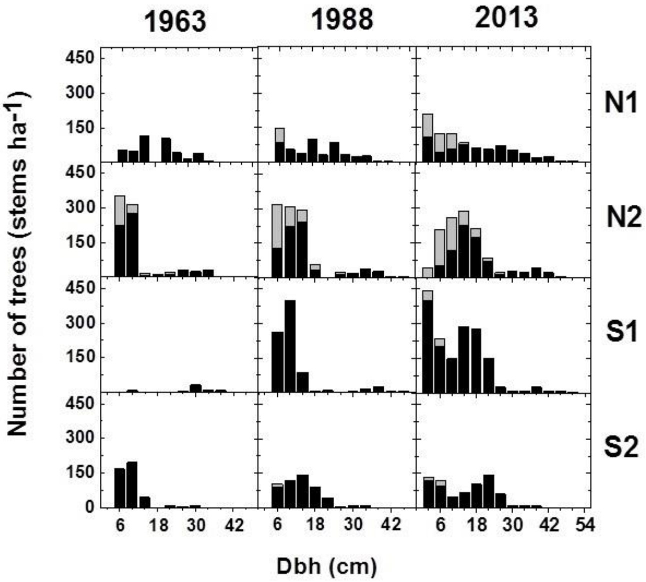

Figure 11. Diameter distribution 1963, 1988, and at inventory 2013, with 4 cm diameter class width. Grey parts represents Norway spruce and black parts Scots pine.

The age distributions for N2, S1, and S2 were quite homogenous, consisting of one or two main age classes. Also in terms of age distribution, N1 was standing out from the other stands, with a more uniform age distribution, consisting of trees in the age span between 20 and 160 years. The wide age span in N1 was however partly from addition of Norway spruce that were the only tree species found in the age span between 20 and 60 years.

Ingrowth of Scots pine saplings was highest at low basal area and decreased with increasing stand density, with no ingrowth in any stand when the basal area exceeded 13 m^2 ha^{-1}. Also for ingrowth of Scots pine trees there was a trend, although not as clear as for saplings, with decreasing number of stems growing into the tree stratum with increasing stand density. The mean annual ingrowth of Scots pine trees was 21.7 trees ha^{-1} yr^{-1} in S1, and between 1.6 and 3.1 trees ha^{-1} yr^{-1} in N1, N2, and S2. Stand S1 had a relatively high level of Scots pine tree ingrowth exceeding 20 stems ha^{-1} yr^{-1} the first half of the reconstruction period, with a flush of ingrowth (>90 stems ha^{-1} yr^{-1}) around 1980. Also N2 had a period with increased ingrowth (exceeding 15 stems ha^{-1} yr^{-1}) in the beginning of the reconstruction period, between 1960 and 1970. Ingrowth of Norway spruce trees mainly took place in the northern stands and was more continuous over time and stand density than ingrowth of Scots pine.

The observed ingrowth dynamics in this study was in line with observed regeneration pulses followed by ingrowth flushes in old-growth Scots pine forests in Sweden (Zackrisson *et al.* 1995, Linder *et al.* 1997) and in Ponderosa pine forests in USA (Boyden *et al.* 2005). Regeneration pulses and subsequent flushes of ingrowth could, according to Zackrisson *et al.* (1995) and Boyden *et al.* (2005), be explained by favourable weather conditions whereas Linder *et al.* (1997) drew the conclusion that major disturbances (forest fires) were the main cause.

The conclusions made by Zackrisson *et al.* (1995) and Linder *et al.* (1997) were, however, not supported by our results. If favourable weather would have been the main cause for regeneration pulses with following ingrowth flushes, we should have found such flushes not only in S1, but also in the other stands.

The stands used in our study had no traces of major disturbances, like forest fires or severe storm damage, nor was there any records of such events during the last 100 years. However, forest operations had taken place in all stands during the last 100 years, and those could probably play a role as major disturbances. By that argument the flush of ingrowth in S1 most likely would have been a result of harvest in 1963, leaving only seed trees, and the more moderate flush in N2 from thinning done in 1947 and 1957.

Annual height growth of Scots pine saplings increased over height with approximately 3 cm yr^{-1} for saplings <1 m to about 4-8 cm yr^{-1} for saplings taller than 2 m. Based on the observed height increment and the assumption that the ingrowth threshold (4 cm dbh) corresponded to a height of 4 m, the estimated time for a sapling to grow from a height of 0.5 to 4 cm dbh would take 60-90 years.

The overall poor correlation between diameter and age distributions, and the observed ingrowth flushes indicated that size heterogeneity in the studied multi-layered Scots pine stands was mainly a result of size stratification among even-aged cohorts, rather than from a continuous ingrowth.

3.2.2 Growth and yield

The northern stands (N1 and N2) had a periodic volume increment (PAI) that was more or less constant in relation to standing volume. In S1 volume increment increased over standing volume up to a standing volume of approximately 100 m^3, where after it levelled off. In S2 PAI was significantly positively correlated ($p<0.05$) with standing volume (Fig. 12). The mean annual volume increment (MAI) during the whole reconstructed period was 1.9, 2.6, 3.8, and 2.0 m^3 ha^{-1} yr^{-1}, which corresponded to 50%, 70 %, 68%, and 44 % of the estimated site productivity in stands N1, N2, S1, and S2, respectively.

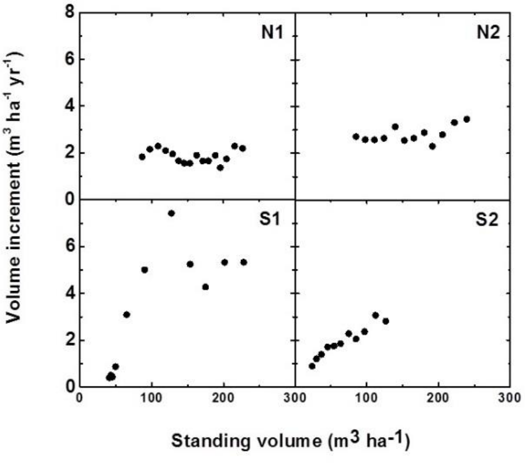

Figure 12. Perodic mean annual volume increment against standing volume in the beginning of each 5 year period.

The positive correlation between standing volume and PAI in the lower part of the volume range and decreasing correlation in the upper part was similar to what have been reported from earlier thinning experiments in even-aged Scots pine stands (Montero *et al*. 2001, Mäkinen and Isomäki 2004). The PAI in even-aged stands is however usually culminating at a level that is 1.5-2.0 times higher than the estimated site productivity where after it declines when approaching the estimated site productivity. Only S1 had a PAI that briefly exceeded the estimated site productivity, whereas PAI culminated below the estimated site productivity in the other stands studied.

4 Conclusions and Management implications

4.1 Norway spruce

If boreal Norway spruce forests spontaneously strive toward an uneven-aged stand structure on low- and medium fertile sites, selection cutting would not be required in order to maintain a suitable stand structure. Removal of trees would not be necessary through the whole dbh range, but could instead be concentrated to the largest and most valuable trees. This would decrease the number of trees removed during each cutting cycle, decrease the harvesting cost per removed m^3 and make management more profitable.

Without conclusive evidence that long-term ingrowth would suffer from a high stand density, and with a positive correlation between standing volume and volume increment, a high standing volume would be recommended when the selection system is applied in boreal Norway spruce forests. In practical management this would require a balance between the length of the cutting cycles, and cost of each selection cutting. Long cutting cycles with heavy harvest intensity in each operation would decrease the harvesting cost per m^3, but would also reduce total production in the stand. With short cutting cycles less standing volume would be removed at each harvest operation, a high standing volume and volume increment would thus be maintained, but harvesting cost would become higher per m^3.

4.2 Scots pine

If multi-layered stand structures in Scots pine forests are created by size stratification, and not continuous ingrowth, they will not be sustainable in the long run without human interference. To maintain a heterogeneous stand structure, a continuous ingrowth would be needed. Even if ingrowth would not have to be annual, recurring flushes of new trees growing into the tree stratum would be required. This would only be possible after heavy reductions of the stand density, in order to secure the establishment, survival, and growth of seedlings and saplings.

With a positive correlation between standing volume and volume increment in multi-layered Scots pine forest, a reduction in stand density to a level were ingrowth would occur, would also heavily reduce the total volume production.

For selection management to be an optimal choice of management in Scots pine forests, other values, e.g. aesthetical or ecological would have to be sufficiently important to compensate for the heavy losses in volume production.

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