Stand Development and Regeneration Dynamics of Managed Uneven-aged *Picea abies* Forests in Boreal Sweden

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Abstract

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Volume increment and ingrowth are important aspects of stand development and regeneration dynamics for determining the effectiveness of uneven-aged silvicultural systems. The main objectives of this thesis were to establish the influence of standing volume on volume increment after different kinds of harvest regimes, the influence of overstorey density on height growth of advance regeneration, and the influence of bilberry (*Vaccinium myrtillus* L.) on spruce regeneration in managed uneven-aged Norway spruce (*Picea abies* (L.) Karst.) forests in boreal Sweden.

Model simulations with 5-year growth iterations and three harvest regimes of diameter-limit, single-tree selection, and schematic harvests were used to investigate the influence of standing volume on volume increment. Additionally, field experiments at two sites, re-inventoried ten years after treatments that had a 3×2 factorial design of three thinning intensities (30, 60, 85% of pre-harvest standing volume) and two types of thinning (harvested larger or smaller trees), were used. The influence of overstorey density on height growth was established using one of the sites that measured height increments of seedlings, saplings, and small trees in the plots. A field investigation was carried out to establish the influence of bilberry on spruce saplings, which cut bilberry stems in 1 m^2 circle plots around treated saplings and their height growth compared to the control saplings with uncut bilberry stems.

Volume increment increased with increasing standing volume, culminated, and eventually declined. The highest volume increment was found for diameter-limit harvests followed by single-tree selection and schematic harvests. For harvesting a residual stand to 50 m^3ha^{-1}, the schematic harvest showed increment losses equalling 25 years of growth. For the field experiments at both sites, standing volume was correlated significantly positively ($p<0.05$) with volume increment. Only for the more productive site, standing volume was correlated significantly negatively ($p<0.05$) with ingrowth. The height increments for all spruce advance regeneration were better correlated with canopy openness than with basal area or standing volume. Treated saplings decreased in height increment compared to the control during the first and second year after cutting bilberry.

In conclusion, volume increment increased with increasing standing volume and harvesting mostly the larger trees in a residual stand with large number of stems and large number of small trees yields high volume increments. At both sites the ingrowth of spruce regeneration was low, but higher than mortality and the number of trees removed, and thus it was sufficient to replace the harvested trees. The cutting of bilberry reduced the height growth of spruce regeneration.

Keywords: advance regeneration, boreal forest, growth modelling, height growth, *Picea abies*, silvicultural systems, stand dynamics, uneven-aged, *Vaccinium myrtillus*, volume increment.

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Appendix

Articles I-IV

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

I. Chrimes, D. and Lundqvist, L. Simulated volume increment of managed uneven-aged *Picea abies* stands in central Sweden. Manuscript.
II. Chrimes, D. Stand development in partially harvested uneven-aged *Picea abies* forests in boreal Sweden. Manuscript.
III. Chrimes, D. and Nilson, C. Overstorey density influence on height increment of *Picea abies* advance regeneration in uneven-aged stands in northern Sweden. Manuscript.
IV. Chrimes, D., Lundqvist, L. and Atlegrim, O. 2004. *Picea abies* sapling height growth after cutting *Vaccinium myrtillus* in an uneven-aged forest in northern Sweden. Forestry 77 (1): 61-66.

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Introduction

Norway spruce (*Picea abies* (L.) Karst.) forests cover a large area of the boreal forest region in Sweden. In fact the Norway spruce forests in Sweden and Finland cover the largest natural spruce area in Europe (Schmidt-Vogt 1991, p. 606). These forests are currently managed primarily with clear-cutting systems. In the mid-nineteenth century until the early 1950s high-grading dominated Swedish forestry (Nilson 2001). Laws were enforced under the Swedish Forestry Act (Anon. 1976), passed in 1948, to forbid the practice of partial harvesting because these partial harvests were deemed as unfavourable for timber production. Nowadays, there is increasing interest in Nordic countries to develop the practice of silviculture and multiple-use of forests. In Sweden, the public seems to favour forests managed by uneven-aged systems (Lindhagen and Hörnsten 2000). Different forms of uneven-aged silviculture have been reported as successful in fulfilling requirements for biodiversity and timber production in spruce forests (Lähde et al. 1999).

To meet the demands and pressures of multiple-use forestry and sustainable forest management, various forms of uneven-aged silviculture are being advocated in Sweden and abroad. Although uneven-aged silvicultural systems, such as single-tree selection, are being advocated as sustainable forest management (Fries et al. 1997), it is still a limited silvicultural practice in Sweden. There are still concerns as to the regeneration and timber production of managed uneven-aged spruce stands in the boreal forests in Sweden (Nilson 2001). More knowledge on the stand development and regeneration dynamics in uneven-aged spruce forests managed by different silvicultural practices in Sweden is therefore needed.

The primary difference in the application of uneven-aged silviculture compared to even-aged silviculture is that foresters harvest only a portion of trees at the stand level at any time. Uneven-aged silviculture requires that, at harvest, foresters remove mature trees to regenerate a replacement age class in proportion to the regeneration area or stand (Nyland 2002). Uneven-aged silviculture comprises many silvicultural systems and the traditional approach is the selection system, which consists of single-tree selection and group selection (Matthews 1991). Single-tree selection harvests to sustain stand growth and control or balance the residual stand density with different size (age) classes and a reverse-J shaped diameter distribution (Matthews 1991). Group selection harvests groups of trees to create regeneration openings, and this practice has usually longer harvest cycles than single-tree selection (Nyland 2002).

Other harvesting regimes applied to uneven-aged stands in European countries are partial harvests. Two kinds of partial harvests are high-grading and diameter-limit harvesting. High-grading is an exploitative harvesting in that only certain species or large and high-valued trees are removed (Nyland 2002). Diameter-limit harvests remove all trees larger than a specified diameter. Diameter-limit harvesting is an application of management that can be applied to both even-aged and uneven-aged stands. It narrows the diameter distribution of stands and does not aim to achieve a reverse-J shaped diameter distribution of the residual stand.

Uneven-aged stands are more complex stand structures than even-aged stands in both the vertical stratification in the stand and spatial distribution of individual trees (Smith et al. 1997). The common characteristics of uneven-aged stands are tree sizes that range from seedling-sapling to large trees, trees of all diameters having large live-crown ratios (Kenefic and Nyland 1999), tree heights that vary markedly with tree diameter, and a multi-layered and multi-storied canopy. According to Meyer (1952), in 1898 de Liocourt published the first numerical studies of diameter distribution in uneven-aged forests and reported that the number of trees in successive diameter classes, from largest to the smallest, form the geometric series m, mq, mq^2, mq^3, and continuing upwards, where q is the diminution ratio coefficient of the series and m is the number of trees in the largest diameter class. The q-ratio is widely accepted and used by foresters in many countries to define uneven-aged stands for two reasons. For the first reason, Meyer (1952) showed that the diameter distribution in natural uneven-aged stands tends toward a constant ratio in terms of the number of trees between successive diameter classes. Secondly, for over one hundred years the q-ratio has been traditionally used to conceptualise and describe diameter distributions for uneven-aged stands. The operational conceptualisation of uneven-aged silviculture is therefore dominated by the diameter distribution of a stand rather than its age structure. The reverse-J shaped diameter distribution of uneven-aged stands are maintained by forest stand dynamics (Oliver and Larson 1996), which is the process of ingrowth of regeneration into the tree stratum, mortality of mostly large mature trees, and a diameter increment that increases with increasing diameter and eventually levelling off (Vanclay 1994).

Table 1. *Growth and yield studies in partially harvested uneven-aged Norway spruce dominated stands*

Author(s) and (Year)	Country	Study Type[a]	Harvest Regime[b]	Harvest Intensity (%)[c]	Standing Volume (m^3ha^{-1})[d]	Influence on Volume Increment[e]
Näslund (1942)	Sweden	Reconstruction	Selection	L to M	100-300	Positive
Sarvas (1944)	Finland	Repeated survey	Above	H	10-180	Positive
Mitscherlich (1952)	Germany	Permanent plots	Selection	L to M	200-600	No
Bøhmer (1957)	Norway	Permanent plots	Selection	L to M	100-200	Positive
Anishin (1975)	Russia	Permanent plots	Above	L to M	130-200	No
Anan´ev and Baryshev (1979)	Russia	Reconstruction	Above	L to M	200-270	No
Spiecker (1986)	Germany	Repeated survey	Selection	L to M	180-350	No
Stolyarov et al. (1988)	Russia	Reconstruction	Above	M	180-250	Positive
Lundqvist (1989)	Sweden	Permanent plots	Selection	L to M	50-300	Positive
Andreassen (1994)	Norway	Repeated survey	Selection	L to M	100-200	Positive
Lundqvist (1994)	Sweden	Reconstruction	Above	H	30-50	Positive
Fuchs (1996)	Germany	Repeated survey	Selection	L to M	280-380	Positive
Bachofen (1999)	Switzerland	Permanent plots	Selection	L to M	250-560	No
Lähde et al. (2002)	Finland	Reconstruction	Selection	M	130-400	Positive
Øyen and Nilsen (2002)	Norway	Reconstruction	Above	H	20-60	No

[a] study carried out on re-measured permanent plots, repeated surveys, or reconstructions of tree growth from increment cores
[b] Selection is single-tree selection (group selection for Bøhmer 1957); Above is the harvesting of mostly larger trees
[c] L, M, and H on average of low (15%), medium (50%), and high (>70%) harvest intensities of pre-harvest standing volumes
[d] average residual standing volumes after harvest
[e] the influence of residual standing volume on volume increment.

Several attempts have been made during the last half of the twentieth century to establish if and to what degree the standing volume affects volume increment in uneven-aged Norway spruce stands. As different results have been reported (Table 1), the issue is not yet settled. In North America, Solomon and Frank (1983) report no definite influence of standing volume on volume increment in managed uneven-aged northern conifer stands in northeastern USA. However, other studies of the growth and yield of managed uneven-aged hardwoods stands in northeastern USA, report a non-linear positive influence of standing volume on volume increment, for example, Duerr and Geovorkianz (1938), Crow et al. (1981), Hansen and Nyland (1987), Guldin and Baker (1988). One reason for the different influences of standing volume on volume increment could be that the varying site conditions, for example the Nordic countries have different site conditions than central European countries, have different affects on the growth of the residual stand.

Different influences of standing volume on volume increment could be a result of different growth responses of residual stands after different kinds of harvests. Lähde et al. (2001) demonstrated that diameter-limit harvests resulted in lower volume increments compared to single-tree selection in uneven-aged spruce stands in Finland. Buonogiorno et al. (2000) showed the opposite by reporting that diameter-limit harvests had higher volume production than selection harvest regimes in uneven-aged northern hardwood stands in northeastern USA. Sterba (2002) forecasted the growth of residual spruce stands in Austria with a growth model, and reported that a target diameter-limit harvest had higher volume increments than a selection harvest regime. Monserud and Sterba (1996) stated that there should be no differences in the effects of different harvest regimes on post-harvest growth because uneven-aged stands should respond to before and after harvest stand density in the same manner. Thus, these different results present an unclear representation of the volume increment after different kinds of harvests in uneven-aged stands.

There is little influence of sapling density on the level of ingrowth into the tree stratum in uneven-aged stands managed by single-tree selection in boreal Sweden (Lundqvist 1995). In spite of this, height growth of regeneration is a major influence on ingrowth. Therefore it is important to establish the influence of the density and structure of the overstorey trees on the height growth of spruce regeneration. Cajander (1934) reported that the main factors affecting the height growth of Norway spruce regeneration in southern Finland are: seedling size, its increment prior to partial harvests, overstorey density, and the harvest interval. Experiences in Finland in the 1920s-1940s after applying partial harvests, however, indicate that stand density has little influence on sapling height increment in uneven-aged Norway spruce stands (Sarvas 1944). This conclusion is supported by studies that show no influence of stand basal area or standing volume on the height growth of regeneration in uneven-aged spruce stands (Nilsen 1988, Lundqvist and Fridman 1996, Nilson and Lundqvist 2001). Other studies show that standing volume has negative effects on the growth of seedlings and saplings in managed spruce shelterwoods (Skoklefald 1967), and unmanaged old-growth spruce stands (Leemans 1991, Hofgaard 1993). Granhus (2001) suggested that local stand density in uneven-aged spruce stands increasingly influences the height growth of advance regeneration, when spruce saplings are growing taller.

One reason for the inconclusive results could be that the structure of the overstorey affects light conditions in forests. Different structures lead to different light intensities and light qualities although the basal areas could be the same (Endler 1993). Greis and Kellomäki (1981) reported that the light conditions affect the height growth of spruce regeneration in the understorey. Estimates of canopy openness can differentiate light conditions under different stand structures (Endler 1993). Therefore growth of regeneration in uneven-aged spruce stands might be better correlated with canopy openness than with stand basal area or standing volume.

Another reason for different results for the influence of overstorey density on the growth of spruce regeneration could be that bilberry (*Vaccinium myrtillus* L.) negatively influences the growth of spruce regeneration (Jäderlund et al. 1997). Growth of spruce regeneration is low when growing in bilberry site types (Sirén 1955). The growth of bilberry after natural and simulated herbivory is faster than that of many other dwarf shrubs, including cowberry (*Vaccinium vitis-idaea* L.) (Tolvanen 1994, Tolvanen and Laine 1997). Light availability influences the total biomass, leaf and shoot morphology, and chemical composition of the bilberry (Laine and Henttonen 1987, Laakos et al. 1990, Atlegrim and Sjöberg 1996). Bilberry plants quickly adjust their growth after reductions in stand density, and this would increase resource competition with spruce regeneration after partial harvesting. Additionally, Pellissier (1993) showed that phenol compounds in bilberry leaves reduces the growth of spruce regeneration. These negative effects that bilberry plants have on the growth of spruce regeneration could explain for the lack of correlation between overstorey density and regeneration growth in uneven-aged spruce stands in boreal Sweden.

Objectives

This thesis deals with stand development and regeneration dynamics after different harvests in managed uneven-aged Norway spruce stands in boreal Sweden. The main objectives were:

1 To establish the influence of standing volume on volume increment after different harvest regimes,
2 To establish the influence of overstorey density on the growth of spruce advance regeneration in partially harvested spruce stands,
3 To establish the influence of bilberry on the height growth of spruce regeneration.

In Article I a growth model was used to analyse and establish the influence of standing volume on volume increment in uneven-aged spruce stands under different kinds of harvests. It was hypothesized that the influence of standing volume on volume increment should be positive. In Article II a permanent field trial was analysed, and it was hypothesized that the influence of standing volume on volume increment should be positive, and that ingrowth should decrease with increasing standing volume. In Article III the influence of overstorey density on spruce regeneration growth was investigated, and the hypothesis was that height growth of the regeneration should be better correlated with canopy openness than with stand basal area or standing volume. In Article IV, height growth of spruce regeneration after cutting bilberry was investigated, and the hypothesis was that bilberry negatively effects the height growth of spruce saplings. Therefore the removal of bilberry should result in an increased growth for the spruce saplings.

Material and Methods

Simulated volume increment (Article I)

The inventory data used in Article I was taken from six permanent plots located in the Siljansfors Experimental Forest, southwest of Mora (60°53'N, 14°25'E, 300 m a.s.l.) in the Darlana County in Sweden. The plots were treated with single-tree selection harvests but did not follow any pre-defined management plan. Norway spruce (*Picea abies* (L.) Karst.) dominated all plots with >90% of stand basal area. Other tree species included Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth.), and white birch (*Betula pubescens* Ehrh.). The ground vegetation was dominated by bilberry (*Vaccinium myrtillus* L.), and the soil moisture was mesic.

At plot establishment, all trees greater than 1.3 m in height were numbered, recorded as standing live or dead, and cross-callipered at permanently marked points at 1.3 m stem height. Only trees larger than 8.5 cm in diameter at 1.3 m height (*d*) were used in this study (cf. Lundqvist 1993). Tree height of sample trees was measured for each plot.

The plots had residual standing volumes of 99 to 256 m^{3}ha^{-1}, with total study length periods of 30 to 57 years and harvest intervals varying from 3 to 11 years. The plots used were sf5.1; sf5.2; sf5.3; sf56.1; sf56.2; and sf82 (cf. Lundqvist 1993). Five of the plots were established from 1921-1925, and the sixth plot in 1959.

The growth model used a stand table projection approach for the model simulations. It included equations for basal area increment, upgrowth, that is the ratio of trees moving into the next size class (cf. Vanclay 1994), and form height. For the basal area increment equation (Article I, Equation II) the variables g_t and g_l represent two-sided and one-sided competition, respectively. The g_t variable is the stand basal area of all trees (diameter ≥8.5 cm) left after each single-tree selection harvest at the beginning of each growth interval. The second variable, g_l, is overtopping basal area, which is the basal area sum for all diameter classes with mean height at least 2 m higher than the target diameter class. To mimic an accelerating shift from two-sided to one-sided competition with increasing stand density, overtopping basal area is multiplied by stand basal area (g_t) squared.

An initial uneven-aged stand with a standing volume of 300 m^{3}ha^{-1} was constructed with a maximum diameter of 45 cm, and a q-ratio of 1.2 for the diameter distribution with 2 cm *d* classes. Three harvest regimes — diameter-limit harvest, single-tree selection, and schematic harvest — harvested trees of the initial stand to reach target volumes of 50, 100, 150, 200, and 250 m^3ha^{-1} (Article I, Figure 2). Diameter-limit harvests removed trees from the largest *d* classes. Single-tree selection harvests removed an almost equal number of trees in each *d* class. Schematic harvests removed a constant proportion of trees in all *d* classes maintaining a 1.2 q-ratio for each target volume.

Five year basal area increment was calculated for each *d* class (Article I, Equation V, VI), then transformed to diameter increment (Article I, Equation VII), and finally used to calculate ingrowth (Article I, Equation VIII).

New diameter distributions were derived using the upgrowth equation and the form height equation. Standing volume (*v*) was calculated for each *d* class (Article I, Equation X), and stand-level volume was calculated by summing the volumes of all *d* classes. Finally, volume increment was the difference between standing volume at the end and the start of growth iteration.

Calculations of growth were done for three, four, five, six, and nine 5-year intervals, with the maximum simulation time of 45 years for a starting volume of 50 m^3ha^{-1}. To analyse the influence of ingrowth, simulations were run both with no ingrowth and with a constant ingrowth of 10 stems $ha^{-1}yr^{-1}$ into the lowest *d* class.

Volume increment and ingrowth (Article II)

The two field experiments used in Article II were located at Ätnarova, south of Gällivare (67°1'N, 20°41'E, 424 m a.s.l.) in northern Sweden, and near Hammerdal, north of Östersund (63°30'N, 15°10'E, 300 m a.s.l.) in central Sweden. About 90 per cent of the standing volume was Norway spruce (*Picea abies* (L.) Karst.) in Ätnarova and 97 per cent in Hammerdal. Other tree species included birch (*Betula pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L.). The time elapsed from previous harvesting activities at each site was about 30 years in Hammerdal and about 60 years in Ätnarova.

Two blocks of seven plots of 0.25 ha in size each established at each site, which equalled a total of fourteen plots per site. In Ätnarova the plots were designated to block I based on a dominant ground vegetation of bilberry (*Vaccinium myrtillus* L.) and to block II for low herbs site type (e.g. *Oxalis acetocella* L., *Maiantemum bifolium* (L.) F.W.Schw.). Plots in Hammerdal were split on the basis of pre-harvest standing volume. Block I had lower standing volumes than block II. The ground vegetation of high herbs, e.g. *Geranium silvaticum* L., *Filipendula ulmaria* (L.) Maxim., *Aconitum septentrionale* Koelle, was the same for all the plots in Hammerdal. Site productivity for Ätnarova was, on average, 2.8 $m^3ha^{-1}yr^{-1}$ and for Hammerdal 5.5 $m^3ha^{-1}yr^{-1}$, both estimated according to Hägglund and Lundmark (1981). Soil moisture at both sites was mesic.

The experiment had a 3×2 factorial design and had 2 replications (blocks), in total 14 plots per site including one untreated control plot per block. Three thinning intensities of 30% (low), 60% (medium), and 85% (high) of initial standing volume and two thinning types, that harvested either larger trees (thinning from above) or smaller trees (thinning from below), were carried out.

In each block, one control plot was randomly selected. The remaining six plots were grouped into three thinning intensity pairs. Thinning intensities were first allotted to the plot pairs, and then the thinning types were allotted within the pairs. All trees with diameter ≥5 cm at 1.3 m height were numbered and cross-callipered at permanently marked points, and heights were measured for randomly sampled trees in each plot. Sample tree volumes were calculated using stem volume functions developed by Brandel (1990) for spruce and birch.

A computer program was used to mark trees for harvest using tree size and local overstorey standing volume around each tree that calculated a value of priority for harvesting a given tree. The tree with the highest priority for harvest was marked and new priority values were then calculated for the remaining trees. The procedure was repeated until the target thinning intensities were reached. Trees marked for harvest were cut in the winter of 1990 for Ätnarova and 1991 for Hammerdal (Article II, Table 1). All plots were re-inventoried in the summer of 2000 and 2001, ten years after the treatments.

Height growth and overstorey density (Article III)

Article III was conducted in the same field experiment in the Ätnarova south of Gällivare, as used in Article II.

In mid-June of 2000, all standing Norway spruce trees with diameter ≥5 cm at 1.3 m in height were cross-callipered and height was measured on sample trees within the gross plots (50×50 m). The stem volume of trees after harvest was calculated according to Article II.

Within each plot, five circle plot centre points were established and marked, positioned like the five on a pair of dice, to measure the Norway spruce regeneration. In the summer of 2000, height increments for the last three years were measured for seedlings (0.1 to 0.49 m in height) within a radius of 3 m (28 m^2 circle plots) from each of the five circle plot centres in each net plot, and for saplings (0.5 to 1.9 m in height) within a radius of 5.64 m (100 m^2 circle plots). Height increments for the last three years were also measured on all small spruce trees (height ≥2.0 m, diameter <5 cm at 1.3 m height) in the central area of 30×30 m (net plot) of the gross plots. Mean annual height increments were then calculated for each net plot.

Hemispherical photographs were taken at the five marked circle plot centres on each of the net plots, with the top of the fish-eye lens at 0.9 m from the forest floor. The shutter speed was set to 1/125 per second, a cable release was used to reduce vibrations, and the camera lens was levelled.

All photographs were cropped with the same total number of pixels within a specified field-of-view area. Canopy openness was then calculated as the percentage of pixels with lightness above a threshold value that represented the sky.

Height growth and bilberry (Article IV)

A field investigation was carried out in Article IV in an uneven-aged Norway spruce (*Picea abies* (L.) Karst.) forest located near Umeå (63°49'N, 19°25'E, 35 m a.s.l.) in northern Sweden. The forest was an uneven-aged stand with about 30 years since the previous harvests. Norway spruce was the dominant tree species with 95 per cent of the standing volume. Other tree species included Scots pine (*Pinus sylvestris* L.) and birch (*Betula pubescens* Ehrh.). The dominant ground vegetation was bilberry (*Vaccinium myrtillus* L.), and the mosses *Pleurozium schreberi* L., and *Hylocomium splendens* (Hedw.) Br. Eur., with sporadic occurrences of cowberry (*Vaccinium vitis-idaea* L.) and *Deschampsia flexuosa* (L.) Trin.

The experiment had a randomised block design with three blocks and five treatments replicated per block. In four treatments (L1, L2, R1 and R2) all bilberry stems were cut at the forest floor level within a 0.56 m radius (1 m^2) around each treated sapling. The fifth treatment was an untreated control where bilberry stems were not cut. In the L1 and L2 treatments, the cut bilberry stems were left on the forest floor while stems were removed in treatments R1 and R2. The procedure was repeated the following year for the L2 and R2 treatments.

Total height (cm) and annual height increment (mm yr^{-1}), for the three last growing seasons (1990, 1991 and 1992) were measured on 45 Norway spruce saplings. The total height of spruce saplings ranged from 43 to 92 cm. The number of bilberry stems was counted within one 0.05 m^2 circular sample plot located in the 1 m^2 treatment area around each sapling, and ranged from 20 to 340 stems per sample plot ($4 \cdot 10^6$ to $68 \cdot 10^6$ bilberry stems per ha).

The Norway spruce saplings were sorted on height and split into three blocks with 15 saplings each. The five treatments were randomly allotted to three saplings in each of the blocks. Before the treatments it was confirmed that no significant differences existed between the treatments within the blocks in sapling mean height and mean annual height increment.

The treatments were first applied on 20 June in 1993, which coincided with the start of height growth of the spruce saplings. For treatments L2 and R2, bilberry cutting was repeated on the same date in the following year. In the late autumn of 1995, height and annual height increments during the last three growing seasons (1993, 1994 and 1995) were measured on all saplings. Measurements of height growth for the growing seasons in 1996, 1997 and 1998 were done in late August of 1998.

Results

In Article I the model simulations showed that the influence of standing volume on volume increment was positive and non-linear. Volume increment peaked at the standing volume of 197 m^3ha^{-1} for the diameter-limit harvest, at 201 m^3ha^{-1} for the single-tree selection, and at 222 m^3ha^{-1} for the schematic harvests (Article I, Figure 4). The maximum predicted current volume increment was 5.8 $m^3ha^{-1}yr^{-1}$ with ingrowth in the simulations and with no ingrowth was 5.4 $m^3ha^{-1}yr^{-1}$ both achieved by diameter-limit harvest (Figure 1). The corresponding increment levels that included ingrowth for single-tree selection and schematic harvests were 5.4 $m^3ha^{-1}yr^{-1}$ and 4.7 $m^3ha^{-1}yr^{-1}$, respectively. In Article II the standing volumes ranged from 32 to 171 m^3ha^{-1} after harvest (Article II, Table 2). After ten years of growth, volume increment was significantly positively ($p<0.01$) correlated with standing volume for both sites (Article II, Figure 1). In Article I the predicted diameter increment increased with increasing diameter, peaked, and eventually decreased (Figure 2). When standing volume increased, diameter increment decreased, and the culmination of maximum diameter increment moved towards the larger diameter classes. Harvesting an uneven-aged stand down to 50 m^3ha^{-1} resulted in an accumulated growth loss equalling 10, 15, and 25 years of full volume production for diameter-limit, single-tree selection, and schematic harvests, respectively (Figure 3).

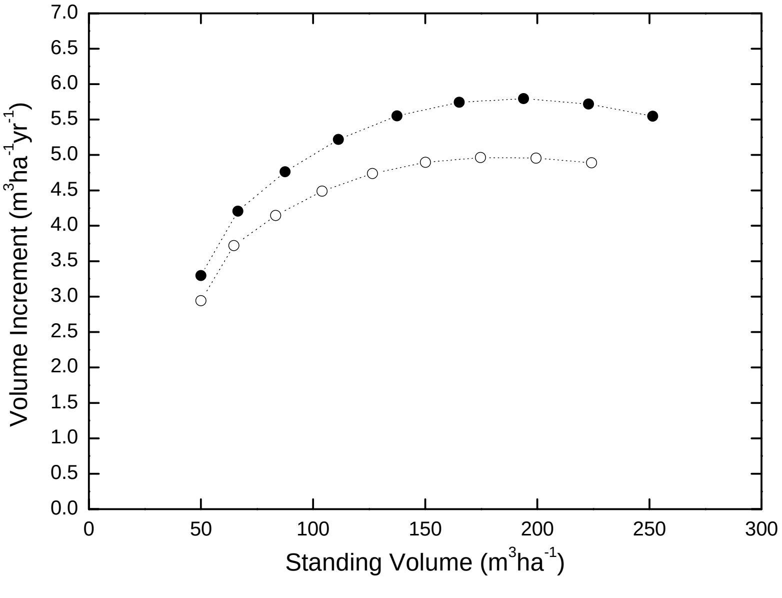

Figure 1. Volume increment ($m^3ha^{-1}yr^{-1}$) for diameter-limit harvest in Article I in the simulations that included an ingrowth of 10 stems $ha^{-1}yr^{-1}$ into the lowest *d* class (●) and no ingrowth (○).

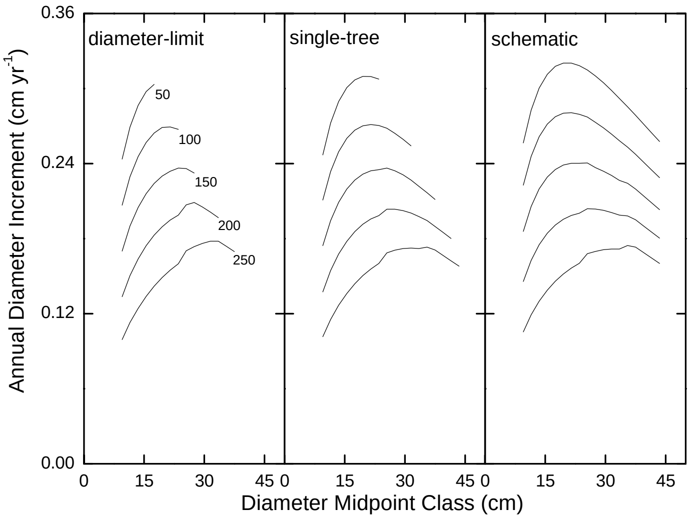

Figure 2. Annual diameter increment (cm yr^{-1}) in Article I in the simulations that included ingrowth for the diameter-limit, single-tree selection, and schematic harvests, respectively. The numbers 50, 100, 150, 200, and 250 denote the target standing volumes (m^{3}ha^{-1}).

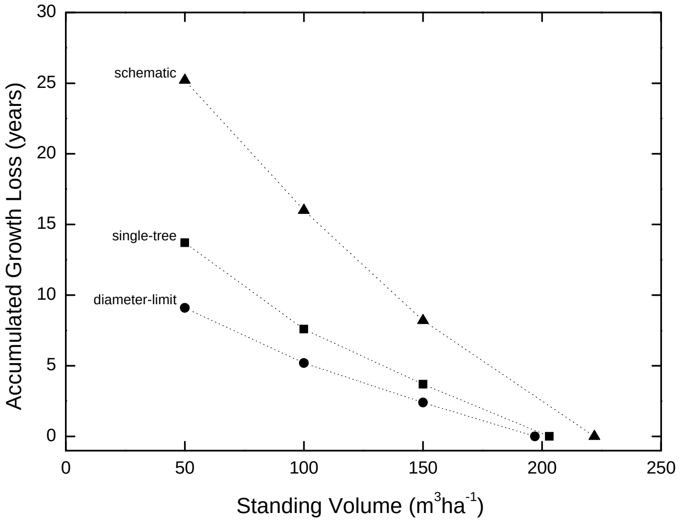

Figure 3. Accumulated growth loss in years in Article I with ingrowth for diameter-limit (●), single-tree selection (■), and schematic harvests (▲).

For harvesting to 50 m^3ha^{-1} results showed that it took 30, 33, and 45 years to reach the maximum volume increments for diameter-limit, single-tree selection, and schematic harvests, respectively (Article I, Figure 6). The mean annual volume increment for this stand restoration period was 56, 74, and 81% of the maximum predicted increment for schematic, single-tree selection, and diameter-limit harvests, respectively.

In Article II, there were no differences in volume increment per tree ($m^3tree^{-1}yr^{-1}$) in the partially harvested stands. However, only the thinning from above plots in Hammerdal showed that volume increment increased with increasing thinning intensity (Article II, Figure 3). The accumulated ten-year mortality after harvest in Ätnarova was 0 to 7.1% of the residual number of stems on 13 plots and 28.6% on one plot, and it was 2.4 to 17.9% in Hammerdal (Article II, Table 2).

In Article II, ingrowth in the treated plots ranged from 2.8 to 9.6 stems $ha^{-1}yr^{-1}$ in Ätnarova and 4.1 to 33.2 stems $ha^{-1}yr^{-1}$ in Hammerdal, respectively (Article II, Figure 2). In Hammerdal standing volume had a significantly negative ($p<0.01$) influence on ingrowth, but it was not significantly negative in Ätnarova.

In Article III, mean height increment for seedlings, saplings, and small trees in the treated plots was 25 mm yr^{-1}, 50 mm yr^{-1}, and 75 mm yr^{-1}, respectively (Figure 4). Mean height increments for the spruce seedlings, saplings, and small spruce trees were better correlated to the canopy openness than to the overstorey basal area followed by overstorey standing volume (Article III, Table 2, 3, and 4). Canopy openness was significantly positively correlated ($r^2=0.39$, $p<0.05$) with overstorey basal areas in the net plots (Article III, Figure 1).

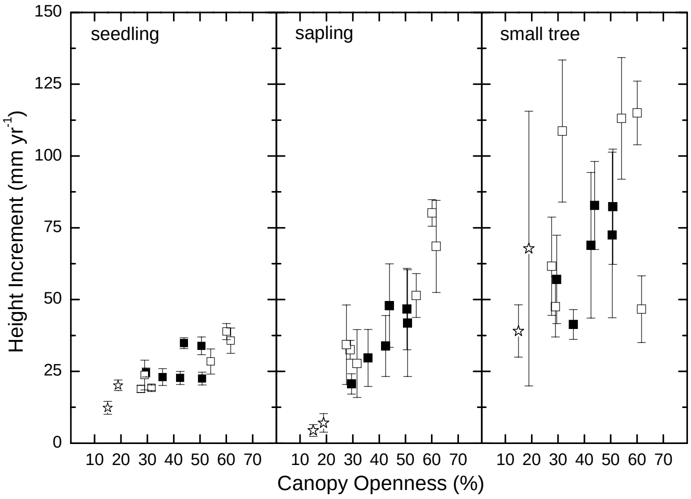

Figure 4. Annual height increment (mm yr^{-1}) in Article III for the spruce seedlings, saplings, and small trees in the control (☆), and the plots treated with thinning from above (■) and thinning from below (□). Lines from the symbols denote the standard deviation for the height increments.

In Article IV the mean treatment response *E* of the treated spruce saplings were significantly ($p<0.05$) lower than for the control in 1994 (Article IV, Figure 1). In 1995, only the *E* value for the L2 treatment was significantly ($p<0.05$) lower than the control. There were no significant differences in *E* between the L and R treatments for any growing season. The combined L2 and R2 treatments that cut bilberry stems twice had lower *E* values for the 1995-1998 growing seasons than the combined L1 and R1 treatments where the bilberry was cut only once (Figure 5).

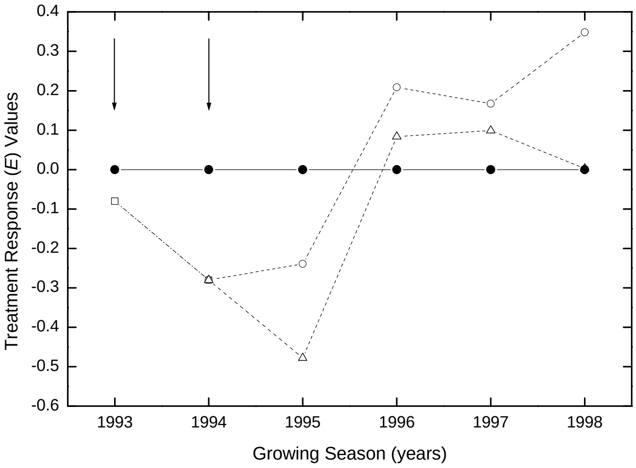

Figure 5. The treatment response (E) of the treated spruce saplings compared to the control for all treatments (☐), for saplings treated once for the L1 and R1 treatments (○), for saplings treated twice for the L2 and R2 treatments (△), and for the control (●) during the 1993-1998 growing seasons in Article IV.

Discussion

Volume increment and ingrowth are important aspects of stand development and regeneration dynamics in managed uneven-aged forests. Standing volume before and after harvest fluctuates between a lower level of standing volume for the residual stand and an upper level of the culminated standing volume before the next harvest. When plotted over time this creates a saw-tooth shaped curve in a wave-like manner. The results in this study showed that volume increment increased with increasing standing volume in managed uneven-aged Norway spruce stands in boreal Sweden, which corroborated the hypotheses (Article I and II). The results were consistent with other studies in managed uneven-aged Norway spruce stands in Sweden (Näslund 1942, Lundqvist 1994), in Finland (Sarvas 1944, Kolström 1993, Lähde et al. 1994, 2001), and in Norway (Bøhmer 1957, Andreassen 1994). They did not, however, correspond with previous studies by Spiecker (1986), and Øyen and Nilsen (2002) who found no influence of standing volume on volume increment in managed uneven-aged spruce stands. Spiecker (1986) studied stands with large standing volumes where all stands were probably at the increment culmination level. Øyen and Nilsen (2002) studied stands treated with heavy partial harvests that left small standing volumes. Rüsch (1983) developed a growth model for managed uneven-aged spruce stands in Switzerland. He reported a non-linear positive influence of standing volume on volume increment, that is increasing stand growth with increasing standing volume towards a peak followed by a decline, and that at a certain increment level the increase in stand density did not influence the increment. He also reported that the highest increment was achieved with a reverse-J shaped diameter distribution. The same kind of non-linear positive relation has also been established for managed uneven-aged hardwoods stands in northeastern USA (Adams and Ek 1974, Crow et al. 1981, Hansen and Nyland 1987, Guldin and Baker 1988).

In Article I the different harvest regimes altered the diameter distribution and had different maximum volume increments at similar standing volumes. Volume increment was highest for the harvests that removed more of the large than small trees. For the residual standing volume of 50 m^3ha^{-1} the diameter-limit harvest removed 40%, single-tree selection removed 51%, and schematic harvest removed 80% of the stems in the original stand. Lowering the number of smaller trees decreased the volume increment of the residual stands (Article I and II). This was consistent with results reported by Näslund (1942). He demonstrated that schematic harvests resulted in lower number of stems and lower volume increments than harvesting mostly the larger trees. Also, Lähde et al. (2001, 2002) observed that harvesting large trees resulted in higher volume increments than if harvesting small trees. Fuchs (1996), in his growth model, reported that volume increment increases non-linearly as the number of stems increases in an uneven-aged spruce forest managed by single-tree selection in southern Germany.

According to the simulation (Article I), volume increment culminated at around 200 m^3ha^{-1} and then eventually dropped. As the six plots used for the study had almost no data for standing volume >200 m^3ha^{-1}, the growth of residual stands above 200 m^3ha^{-1} was an extrapolation. A culmination point and a subsequent decrease in net volume increment can be expected if mortality increases when standing volume increases. However, the model did not include mortality. The results thus conflicts with accepted knowledge on forest growth dynamics. The design of the competition variables and the lack of inventory data for large standing volumes probably contributed to a combined effect for the lowering of volume increment after its peak.

For all stands studied, diameter increment increased slowly with increasing diameter and eventually levelled off (Article I). This corresponded with previous studies in managed uneven-aged spruce stands (Spiecker 1986, Andreassen 1994, Bachofen 1999). With increasing stand basal area, diameter increment in the simulated stands culminated at increasingly larger diameters (Article I). This was consistent with observations by Wykoff (1990), who found that smaller trees decreased their growth more than larger trees with increasing basal area in conifer-dominated stands in the northern Rocky Mountains USA.

The model simulations used a constant ingrowth of 10 stems $ha^{-1}yr^{-1}$ into diameter ≥8.5 cm at 1.3 m height (Article I). Previous analysis of the same plots, as used for the model in Article I showed that the average ingrowth level was 4.9 to 16.9 stems $ha^{-1}yr^{-1}$ (Lundqvist 1993). However, Kolström (1993) assumed that the influence of residual standing volume on ingrowth was negative and non-linear in his growth model for managed uneven-aged spruce stands. In Article II the ingrowth into diameter >5 cm at 1.3 m height was relatively constant for the low productive site, Ätnarova. However, the ingrowth decreased with increasing standing volume for the high productive site, Hammerdal. For a stand with the standing volume of 50 m^3ha^{-1}, the volume increment was twice as high with the addition of the ingrowth after three growth iterations, that is 15 years, especially for the schematic harvest (Article I). The inconclusive results for the different influences of standing volume on ingrowth in Article II showed that more research is needed to clarify the issue.

Height growth of the regeneration has a major influence on ingrowth rates and can be used to predict changes in the level of ingrowth for uneven-aged stands (Lundqvist 1995). In Article III, height growth of spruce regeneration was better correlated with canopy openness than with stand basal area or standing volume. The weak correlation between height growth of spruce saplings and stand basal area corresponded with results from previous studies in managed uneven-aged spruce stands (Fridman and Lundqvist 1996, Nilson and Lundqvist 2001). The results also supported Bachofen (1999) who concluded that standing volume and regeneration height growth was not correlated, even for small standing volumes. Mitchell and Popowich (1997) and Brandies et al (2001) both concluded that basal area is a weak estimator of canopy openness for denser stands. The results in Article III corresponded with this because the large basal areas in the treated plots were not correlated with canopy openness. Since the correlation between canopy openness and basal area was weak and differences in height growth of spruce regeneration with different estimates of canopy openness were small (Article III), increases in the level of ingrowth after schematic harvesting to 50 m^3ha^{-1} might be almost negligible. However, for a more productive site ingrowth might increase after harvest (Article II).

In Article II, ingrowth was generally higher than mortality of larger trees and the number of trees removed. This indicated that even though spruce seedlings and saplings were growing slowly, the ingrowth level was sufficient to replace the harvested trees. This corresponded with Lähde et al (2002) who reported that although some of the seedlings, saplings, and small trees died during harvest operations, an average ingrowth (trees growing into diameter ≥8.5 cm at 1.3 m height) of 7.3 stems $ha^{-1}yr^{-1}$ was sufficient to replace the trees harvested.

Fine roots of natural spruce regeneration are positioned lower in the soil humus layer than the roots and rhizomes of bilberry plants, and a bilberry rhizome extends up to 10-15 m in length (Flower-Ellis 1971). Cutting of the bilberry stems reduced the height growth of spruce saplings. This could be explained by at least two factors: the dying of the bilberry roots promoted microbial immobilization of mineral nutrients (Newman and Eason 1989); or chemicals leaked down from the dying roots which harmed the spruce directly or made the soil less fertile (cf. Zackrisson et al. 1997). The study in Article IV did not attempt to identify the interference mechanism, but the results indicated that the interaction between bilberry and spruce is complex. Further investigations are needed to verify if cutting bilberry reduces the growth of spruce saplings.

Management Implications

For uneven-aged silviculture, forest management requires the establishment of harvest cycles and planning of harvest regimes. This thesis implies that standing volume and ingrowth are important criteria for forest managers. The influence of standing volume on volume increment was established as positive in managed uneven-aged spruce stands in boreal Sweden. Ingrowth of spruce regeneration was low, but it was sufficient to replace the harvested trees. Besides standing volume, volume increment is influenced by the diameter distribution and number of stems. Large number of small trees and large number of stems in the stand resulted in high volume increment. This suggests that foresters should apply moderate harvest intensity and harvest mostly large trees to safeguard a high level of volume increment for the next harvest. This implies that if the number of stems is low, the harvest cycle should be prolonged.

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References

Adams, D.M. and Ek, A.R. 1974. Optimizing the management of uneven-aged forest stands. Can. J. For. Res. 4: 274-287.

Andreassen, K. 1994. Development and yield in selection forest. Medd. Skogforsk 47: 1-37.

Anan´ev, V.A. and Barysheva, G.I. 1979. Dinamika tekushchikh prirostov v el´nikakh, proidennykh vyborochnymi rubkami (The dynamics of current increment in Norway spruce after selective cutting). Lesovedenie 4:14-19. (in Russian.)

Anishin, P.A. 1975. Peculiarities of current increment in different-aged Piceetum of the middle Taiga. Lesovedenie 3: 3-11. (in Russian with English summary.)

Anon. 1976. Skogsvårdslagen med tillämpningsanvisningar. Skogsstyrelsen. Nordstedts, Stockholm.

Atlegrim, O. and Sjöberg, K. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. For. Ecol. Manage. 86: 39-50.

Bachofen, H. 1999. Equilibrium, structure and increment in selection forest stands. Schweiz. Z. Forstwes. 150: 157-170. (in German with English summary.)

Bøhmer, J.G. 1957. Bledningsskog II. Tidskrift for skogsbruk 65: 203-247. (in Norwegian with French summary.)

Brandel, G. 1990. Volume functions for individual trees: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula pendula* and *Betula pubescens*). Sveriges lantbruksuniversitet, Institutionen för skogsproduktion. Garpenberg. Rapport 26. 183 pp. (in Swedish with English summary.)

Brandeis, T.J. Newton, M. and Cole, E. 2001. A comparison of overstory density measures for describing understorey conifer growth. For. Ecol. Manage. 152: 149-157.

Buonogiorno, J., Kolbe, A. and Vasievich, M. 2000. Economic and ecological effects of diameter-limit and BDq management regimes: simulation results for northern hardwoods. Silva Fennica 34: 223-235.

Cajander, E.K. 1934. Kuusen taimistojen vapauttamisen jälkeisetä pituuskasvutsa. Referat: Über den Höhenzuwachs der Fitzchenpflanzenbestände nach der Befreiung. Commun. Inst. For. Fenn. 19, 1-53. (in Finnish with German summary.)

Crow, T.R., Jacobs, R.D., Oberg, R.R. and Tubbs, C.H. 1981. Stocking and structure for maximum growth in sugar maple selection stands. North Central Forest Experimental Station. USDA Forest Service Res. Paper NC-199.

Duerr, W.A. and Geovorkianz, S.R. 1938. Growth prediction and site determination in uneven-aged timber stands. J. Agric. Res. 56: 81-98.

Endler, J.A. 1993. The color of light in forests and its implications. Ecol. Monograph 63: 1-27.

Flower-Ellis, J.G.K. 1971. Age structure and dynamics in stands of bilberry. Ålder, struktur och dynamik hos blåbärsbestånd. Institutionen för växtekologi och marklära, Skoghögskolan. Rapporter och uppsatser 9. Rotobeckmen, Stockholm. 108 pp. ISBN 99-090-7799-X.

Fries, C., Johansson, O., Pettersson, B. and Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. For. Ecol. Manage. 94: 89-103.

von Fuchs, A. 1996. Forest management of the Kruezberg selection forest. Forstwes. Cbl. 115: 51-62. (in German with English summary.)

Granhus, A. 2001. Partial cutting in Norway spruce: impacts on advance regeneration and residual stand. PhD Dissertation. Agricultural University of Norway., Department of Forest Sciences, Ås, Norway. 30 pp. ISBN 82-575-0461-0.

Greis, I. and Kellomäki, S. 1981. Crown structure and stem growth of Norway spruce undergrowth under varying shading. Silva Fenn. 15: 306-322.

Guldin, J.M. and Baker, J.B. 1988. Yield comparisons from even-aged and uneven-aged loblolly-shortleaf pine stands. South. J. Appl. For. 12: 107-114.

Hägglund, B. and Lundmark, J.-E. 1981. Handledning i bonitering med Skogshögskolans boniteringssystem, Del 1-3 Diagram och tabeller. Skogsstyrelsen, Jönköping, Sweden, 244 pp.

Hansen, G.D. and Nyland, R.D. 1987. Effects of diameter distribution on the growth of simulated sugar maple stands. Can. J. For. Res. 17: 1-8.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. J. Veg. Sci. 4: 601-608.

Jäderlund, A., Zackrisson, O., Dahlberg, A. and Nilsson, M.-C. 1997. Interference of *Vaccinium myrtillus* on establishment, growth, and nutrition of *Picea abies* seedlings in a northern boreal site. Can. J. For. Res. 27: 2017-2025.

Kenefic, L. and Nyland, R. 1999. Sugar maple height-diameter and age-diameter relationships in an uneven-aged northern hardwood stand. North. J. Appl. For. 16: 43-47.

Kolström, T. 1993. Modelling the development of an uneven-aged stands of *Picea abies*. Scand. J. For. Res. 3: 373-383.

Laakos, S., Lehtinen, P. and Raatikainen, M. 1990. The influence of spruce and pine in the cover values, flowering and berry yields of the bilberry (*Vaccinium myrtillus* L.). Mem. Soc. pro fauna et flora Fen. 66: 47-53. (in Finnish with English summary.)

Lähde, E., Laiho, O. and Norokorpi, Y. 1999. Diversity-oriented silviculture in the boreal zone of Europe. For. Ecol. Manage. 118: 223-243.

Lähde, E., Laiho, O. and Norokorpi, Y. 2001. Structure transformation and volume increment in Norway spruce-dominated forests following contrasting silvicultural treatments. For. Ecol. Manage. 151: 133-138.

Lähde, E., Laiho, O., Norokorpi, Y. and Saksa, T. 1994. Structure and yield of all-sized and even-sized conifer dominated stands on fertile sites. Ann. Sci. For. 51: 97-109.

Lähde, E., Laiho, O., Norokorpi, Y. and Saksa, T. 2002. Development of Norway spruce dominated stands after single-tree selection and low thinning. Can. J. For. Res. 32: 1577-1584.

Laine, K.M. and Henttonen, H. 1987. Phenolics/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. Oikos 50: 389-395.

Leemans, R. 1991. Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forests in central Sweden. Vegetatio. 93: 157-165.

Lindhagen, A. and Hörnsten, L. 2000. Forest recreation in 1977 and 1997 in Sweden: changes in public preferences and behaviour. Forestry 73: 143-153.

Lundqvist L. 1989. Use of selection system in Norway spruce forests - changes in the stand structure, volume increment, ingrowth and regeneration on experimental plots managed with single-tree selection. The Swedish University of Agricultural Sciences, Department of Silviculture, PhD Dissertation. 22 pp. ISBN 91-576-3837-3. (in Swedish with English summary.)

Lundqvist, L. 1993. Changes in the stand structure on permanent *Picea abies* plots managed with single-tree selection. Scand. J. For. Res. 8: 510-517.

Lundqvist, L. 1994. Growth and competition in partially cut sub-alpine Norway spruce forests in northern Sweden. For. Ecol. Manage. 65: 115-122.

Lundqvist, L. 1995. Simulation of sapling population dynamics in uneven-aged *Picea abies* forests. Ann. Bot. 76: 371-380.

Lundqvist, L. and Fridman, E. 1996. Influence of local stand basal area on density and growth of regeneration in uneven-aged *Picea abies* stands. Scand. J. For. Res. 11: 364-369.

Matthews J.D. 1991. Silvicultural systems. Paperback edition. Clarendon press, Oxford. ISBN 0-19-854670-X.

Meyer, H.A. 1952. Structure, growth, and drain in balanced uneven-aged forests. J. Forestry 50: 85-92.

Mitchell, J.E. and Popovich, S.J. 1997. Effectiveness of basal area for estimating canopy cover of ponderosa pine. For. Ecol. Manage. 95: 45-51.

Mitscherlich, G. 1952. Der Tannen-Fichten-(Buchen)-Plenterwald. Schriftenreihe der Badischen Forstlichen Versuchsanstalt, Freiburg im Breisgau. Heft 8. 42 pp.

Monserud, R.A. and Sterba, H. 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. For. Ecol. Manage. 80: 57-80.

Näslund, M. 1942. Den gamla norrländska granskogens reaktionsförmåga efter genomhuggning. Medd. Statens Skogsförsöksanstalt. Häfte 33(1). 180 pp. (in Swedish with German summary.)

Newman, E.I. and Eason, W.R. 1989. Cycling of nutrients from dying roots to living plants including the role of mycorrhizas. In: Clarholm, M. and Bergström, L. (eds) Ecology of arable land. Kluwer, Dordrecht. 133-137 pp.

Nilsen, P. 1988. Selective cutting in mountain spruce forests – regeneration and production after earlier cuttings. Norsk. Inst. Skogsf., Rapport 88. 26 pp. (in Norwegian with English summary.)

Nilson, K. 2001. Regeneration dynamics in uneven-aged Norway spruce forests with special emphasis on single-tree selection. Doctoral Thesis 209. The Swedish University of Agricultural Sciences. Department of Silviculture, Umeå Sweden. 24 pp. ISBN 91-576-6093-X.

Nilson, K. and Lundqvist, L. 2001. Effect of stand structure and density on development of natural regeneration in two *Picea abies* stands in Sweden. Scand. J. For. Res. 16: 253-259.

Nyland, R. 2002. Silviculture: concepts and applications. Second Edition. McGraw-Hill Companies, Inc., New York. ISBN 0-07-366190-2.

Oliver, C.D. and Larson, B.C. 1996. Forest Stand Dynamics. Update Edition. Jon Wiley & Sons Inc., New York. ISBN 0-471-13822-9.

Øyen, B-H. and Nilsen, P. 2002. Growth effects after mountain forest selective cutting in southeast Norway. Forestry 75: 401-410.

Pellissier, F. 1993. Allelopathic effect of phenolic acids from humic solutions on two spruce mycorrhizal fungi: *Cenoccum graniforme* and *Laccaria laccata*. J. Chem. Ecol. 19: 2105-2114.

Rüsch, V.W. 1983. Hiebsatzweiser in der Praxis. Schweiz. Z. Forstwes. 134: 109-129. (in German with French summary.)

Sarvas, R. 1944. The effect of saw-timber selection on private forests in southern Finland. Comm. Inst. For. Fenn. 33. 268 pp. (in Finnish.) ISBN 99-087-2307-3.

Schmidt-Vogt, H. 1991. Die Fichte: ein Handbuch in zwei Bänden. Band II/3, Waldbau - Ökosysteme - Urwald - Wirtschaftswald - Ernährung - Düngung - Ausblick. Verlag Paul Parey. Hamburg and Berlin. ISBN 3-490-09716-5.

Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta For. Fen. 62: 1-363.

Skoklefald, S. 1967. Release of natural Norway spruce regeneration. Medd. Norske Skogsfør. 85: 381-409. (in Norwegian with English summary.)

Smith, D.M., Larson, B.C., Kelty, M.J. and Ashton, P.M. 1997. The practice of silviculture: Applied forest ecology. Ninth Edition. Wiley and Sons Inc. New York. ISBN 0-471-10941-X.

Solomon, D.S. and Frank, R.M. 1986. Growth response of managed uneven-aged northern conifer stands. USDA For. Ser. N.E. For. Exp. St. Paper 517.

Spiecker, H. 1986. Growth of fir (*Abies alba* Mill.) and spruce (*Picea abies* Karst.) in selection forest research plots in the Black Forest from 1950 to 1984. Allgemeine Forst – und Jagdzeitung. 157: 152-163. (in German with English summary.)

Sterba, H. 2002. Forest inventories and growth models to examine management strategies for forests in transition. Forestry 75: 411-418.

Stolyarov, D.P., Dekatov, N.N., Minyaev, V.N. and Pegov, L.A. 1988. Prognozirovanie rosta raznovozrastnykh el´nikov posle vyborochnykh rubok (Forecasting the growth of uneven-aged spruce forests after selective cutting). Lesnoe khozyaistvo 8:13-15. (in Russian.)

Tolvanen, A. 1994. Difference in recovery between a deciduous and evergreen ericaceous clonal dwarf shrub after simulated aboveground herbivory and belowground damage. Can. J. Bot. 72: 853-859.

Tolvanen, A. and Laine, K. 1997. Effects of reproduction and artificial herbivory on vegetative growth and resource levels in deciduous and evergreen dwarf shrubs. Can. J. Bot. 75: 656-666.

Vanclay, J.K. 1994. Modelling forest growth and yield. Applications to mixed tropical forests. CAB International. Wallingford, UK. ISBN 0-85198-913-6.

Wykoff, W.R. 1990. A basal area increment model for individual conifers in the Northern Rocky Mountains. For. Sci. 36: 1077-1104.

Zackrisson, O., Nilsson, M.-C., Dahlberg, A. and Jäderlund, A. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. Oikos 78: 209-22.