Thinning of Norway spruce

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Abstract

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The objective of this thesis was to investigate volume and quality outcome from different thinning strategies in monocultures with Norway spruce. Two different experiments were set up at the Tönnersjöheden experimental forest in south west Sweden. In the first experiment, the combined effect of spacing and thinning type on timber quality and the spacing effect on volume production was investigated (paper I). In the second experiment, the initial growth response after thinning was investigated during three growing seasons in a 33 year old stand after removal of 0, 30- and 60% of the basal area (paper II and III). In a survey study, covering southern Sweden, the amount of thinning injuries to stems and coarse roots in spruce monocultures thinned with harvesters and forwarders was investigated (Paper IV).

The total volume production was rather similar in the three spacings, 246, 226 and 232 m3 respectively (paper I). The quality of individual trees was to a large extent related to diameter at breast height and not to spacing per se. In the second experiment, heavy thinning increased soil moisture, light transmittance and soil temperature, and hence the nitrogen mineralization. The nitrogen content in the needles and the needle efficiency increased after heavy thinning but there were only small effects on those parameters for normally thinned plots. The current annual volume production after thinning showed an initial drop during the first two growing seasons but was slightly higher during the third growing season compared to the unthinned control. Heavy thinning increased resource allocation to the stem base. The basal area increment for the largest trees (100-400 stems per hectare) increased with increasing thinning intensity (Paper II & III). The risk for damage from heavy winds and wet snow showed a linear increase with thinning intensity. The frequency of injured trees was high (10-15%).

The main finding is that there is a large “biological window” for silvicultural regimes in terms of their effect on total volume production but the thinning regime has a major impact of the risk for abiotic and biotic damages.

Key words: *Picea abies*, volume production, timber quality, spacing, eco-physiology, stem form, injuries, storm damages, snow damages

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To Jenny, Ida and Vilda

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Appendix

Paper I-IV

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

I. Pfister, O., Wallentin, C., Nilsson, U. & Ekö, P.-M. 2007. Silviculture in Norway spruce (*Picea abies*) stands with wide spacing – Effects on wood quality. (Under revision, Scandinavian Journal of Forest Research)

II. Wallentin, C., Nilsson, U. 2007. Thinning in Norway spruce: Short-term effects of thinning grade on growth, light, nutrient and water regimes in a 33-year old stand in Sweden. (Manuscript)

III. Wallentin, C. 2007. Thinning of Norway spruce: Short-term effects of thinning grade on individual tree growth, total aboveground biomass production and needle efficiency in a 33-year old stand in Sweden. (Manuscript)

IV. Wallentin, C., Nilsson, U. & Nordfjell, T. 2007. Damage to stems and roots following mechanised thinning in Norway spruce plantations in southern Sweden. (Submitted to Silva Fennica)

Introduction

If a forest stand contains so many trees that they strongly compete with each other for growth resources, such as light, water and/or nutrients, cutting some of them may allow the remaining trees to grow faster than they did before the cutting. This may or may not improve the stand. According to the Swedish Forest Association's Technical Forestry Vocabulary (Anon., 1994), thinning is defined as: stand improvement under extraction of wood. In English vocabulary there is a distinction between commercial thinning and pre-commercial thinning. The former referring to the profitable removal of trees to improve the remaining stand, while the latter refers to early removals of trees that generally has little or no commercial value. Pre-commercial thinning in very young stands is sometimes referred to as "cleaning". Here, thinning will be regarded as the removal of trees from a stand in order to improve the performance of the remaining trees and generate a net income. However, it should be noted that regardless of whether the Swedish or English definitions are used, there is no clear boundary between pre-commercial thinning and thinning.

Three main features are most important for describing a thinning regime: the type, grade and intensity (Assmann, 1970). Thinning type in this context mainly depends on whether the cut trees are larger or smaller than the remaining trees (thinning from below or thinning from above, respectively), but it may also refer to the geometrical pattern of cutting (selective thinning or row thinning). The grade of a thinning is a measure of the amount of material removed, and one of the best descriptors is the amount of basal area (or volume) removed relative to the basal area (or volume) before thinning. However, for comparisons of thinning programmes in which several thinnings are done at different times the percentage of basal area removed in each cutting is not a suitable descriptor. Therefore, the periodic mean basal area (at a given site index and relative to another thinning grade) is sometimes used as an indicator of the thinning grade. The periodic mean basal area can be calculated using the following formula (Assmann, 1970):

$$\text{Periodic mean basal area} = ((g1+G1)/2)m1+(g2+G2)/2)m2\ldots.+((gn+Gn)/2)mn)/(m1+m2+\ldots mn)$$

where: g represents the basal area at the beginning of an observation period, G the basal area at the end of that observation period and m is the number of years in each period (indicated by subscript 1, 2 ,…., n).
Thinning intensity consist of two part, timing and frequency. Timing refers to the age (or top height) at which thinning commences and frequency refers to mean interval between thinning occasions. According to Assmann (1970), an "extensive" thinning starts at over 12 m mean height and the average cutting cycle is five years or more and a "highly intensive" thinning programme start before 8 m mean height and the average cutting cycle is less than three years.

Thinning should never be considered in isolation from other silvicultural practices. Possible thinning regimes are heavily influenced by previous steps, such as the regeneration and pre-commercial thinning, and the thinning carried out sets the conditions for further thinnings and/or regeneration options. Traditionally the following motives for thinning are often highlighted (Andersson, 1911; Wahlgren, 1914; Juhlin Dannfelt, 1954; Fries, 1961; Anon., 1969; Söderström, 1980).

- To enhance diameter growth of individual trees
- To improve wood quality of remaining trees
- To avoid self-thinning
- To obtain some income early in the rotation period

The focus in this thesis is on issues that have been studied for more than 100 years. Even in the early days of the Swedish Institute of Experimental Forestry Alexander Maass noted that issues related to the effects of initial spacing and thinning regimes on production and profitability in Swedish plantations were of great concern (Maass, 1904). Many wise words have been written and spoken about these matters both before and since then. Why then present yet another contribution, another dust collector? Sound decision-making in commercial forestry requires relevant knowledge about the biological processes involved and the impact of current and future conditions. Each new generation should question traditional orthodoxies regarding forest stand dynamics, and hopefully develop new knowledge of forest biology, while at the same time retaining previously acquired information not disproved.

Plan of this thesis

In the introduction of this thesis I briefly outline the history of thinning practices in Sweden (mostly adopted from Germany and Denmark). The next section reviews literature about initial spacing in relation to stem volume production, tree properties (wood quality) and profitability. The following part, about thinning, is rather similar to that about initial spacing but focuses more on volume production and less about wood quality. The effect of increased initial spacing on tree properties and wood quality is rather similar to the effect of increased spacing after thinning, simply further up the stem. The effect of thinning on wood quality also includes the effect of selection.

Thereafter, attempts are made to increase the understanding of the thinning reaction. That is the eco-physiological responses to thinning (light, water and nutrients). Forestry is almost certain to face serious changes and challenges in the future, notably related to potential global climate changes and attempts to ameliorate their effects. Such changes are affecting not only the growth of trees and stands, but potentially every aspect of forestry, including fundamental silvicultural aims and methods (Jarvis, Ibrom & Linder, 2005; Kellomäki & Leinonen, 2005; Eriksson, 2006). It has been claimed (Lagergren, 2001) that traditional growth and yield models based on empirical data (Eriksson, 1976; Ekö, 1985; Agestam, 1985, Persson, 1992) with low time resolution (five years) and lack of relationships with physical driving variables would be less valuable as predictors of growth in the future due to changing environment. However, I strongly believe that yield tables, empirical growth models and classical long term thinning experiments gives and will continue to give better guidance for forestry practice than short time measurements of changes in eco-physiology in relation to different thinnings. However, process-based models could be much useful in areas lacking god empirical data (Almeida, Landsberg & Sands, 2004) and the combination of conventional models and process-based models might provide increased predictive power and flexibility (Landsberg, 2003). To implement traditional silvicultural knowledge in a changeable environment, high levels of both biological and silvicultural understanding are essential. The combination of classical forest production research with tree physiology should provide a valuable road map for meeting such future challenges.

The applied Silviculture affects the risk for biotic and abiotic damages. In the final section of the introduction I will give background information about the risk for storm and snow damages in relation to thinning and initial spacing. The risk for root- and butt rot infection (*Heterobasidion* spp.) in relation to applied silviculture is also discussed. Finally, injuries to stem and coarse roots on remaining trees after thinning and subsequent rot infection are evaluated.

Historical background

Thinning in Germany

Thinning in young stands to improve the future crop trees was widely adopted, and legally required, in some German states, in the 16th century. The following two hundred years saw the opposite trend, and thinning in young stands was even prohibited in order to encourage wildlife (Schotte, 1912; Brandl, 1992). Thinning in even-aged stands is dependent on a silvicultural system with clear-cutting followed by plantation or a relatively brief step-wise removal of the old stand combined with natural regeneration. Systematic clear-cutting was first adopted in Germany based on ideas proposed by Georg Ludvig Hartig (1764-1837) (1795) and Heinrich von Cotta (1763-1844) (1817). The main rationale of their system was to promote long-term cutting sustainability by obtaining stands with an even age class distribution. Thus, Cotta and Hartig, once again advocated thinning, and some decades later research plots were established to address questions about stand development and volume production (Brandl, 1992). The most influential of the German foresters in the 19th century advocated light thinning grades and thinning from below (Schotte, 1912). In most cases, only dead and/or suppressed trees were allowed to be cut. This, usually expensive, system was questioned in the early 19th century by Reventlow in Denmark (Reventlow, 1879; Oppermann, 1928) and in the late 19th century in Germany by Borggreve (Wallmo, 1897).

Thinning in Sweden

The history of thinning in Sweden varies in different parts of the country. Southern, central and northern Sweden has their own history but there are also many connections between them. In the 19th century the industry related to timber, pulpwood and other products started to become important, leading to the development of a more sophisticated regulatory system. Albeit at a limited scale, the clear-cutting system developed in Germany by Hartig and von Cotta (as adapted for Swedish conditions by af Ström; (Wahlgren, 1928; Carbonnier, 1978)) began to be applied in southern Sweden in forests owned by the state. However, the suitability of the state as a forest owner was questioned. Other important forest owners interested in silviculture were larger estates and the mining industry (Albertsson, 2000). The silvicultural systems adopted were usually imported from Denmark or Germany (Eliasson, 2002). Danish foresters were employed on the largest estates in the southern part of the country and German foresters did important work in central Sweden (Enander, 2000; Brynte, 2002). The stands that developed after clear cutting were usually quite dense, and, if thinned at all, they were thinned from below, with removal solely of dead or suppressed trees (Sandbladh, 1867; Wallmo, 1897). The principal aim was to maximise volume production. The first thinning was often initiated rather late (30-50 year), and the time between thinnings were usually 15-20 years (Juhlin Dannfeldt, 1959). This thinning programme was similar to that advocated by Georg Ludvig Hartig (Eliasson, 2002).

To be economically feasible thinning activities need a market for small sized trees. During the 19th century, due to the dependence of various industries, notably the iron industry, on charcoal for their production there was a market even for small logs (Nyblom, 1959, Olsson, 1993). One of the most important changes, with profound implications for thinning in the second half of the 19th century, was the establishment of pulp and paper mills. Wood products, iron and steel accounted for 60% of Swedish exports, by value, between 1851 and 1855. Pulp and paper made negligible contributions, but 30 year later, they accounted for around 5% of the export value and a further 30 years later, the figure was almost 20% (Fridlizius, 1963 as quoted by Björklund, 1988 and Olsson, 1993). Although there was a market for small trees and expert opinion recommended thinning (Ström, 1822, 1830; Sandbladh, 1867; Georgsson Hjort, 1869) it was generally neglected (Carbonnier, 1936). This is illustrated in the investigation by Juhlin Dannfelt (1959) based on data from the Swedish National Board of Forestry concerning the area thinned in public forests in the year 1878. Only 0.2% of the forests were thinned during that year and thinning was not practiced at all in the northern part of the country.

Sweden's share of the world market for chemical or mechanical pulpwood was consistently greater than its share of the market for sawn goods during the early 20th century (Streyffert, 1931). The pulp and paper industry used the same kind of small logs as those previously used for charcoal production, and together with reductions in the top diameter for logs used as saw timber there was increasing interest in thinning (Pettersson, 1955). In the first decades of the 20th century, a more active thinning schedule was proposed by Schotte (1912). The first thinning was initiated earlier, the thinning grade increased, the time between two consecutive thinnings decreased and the cuttings were oriented higher in the diameter distribution (Juhlin Dannfeldt, 1959). Thinning programmes in which the times between thinnings are short, and the percentage of standing basal area or standing volume removed in each thinning is low, are probably optimal for maximising the production of merchantable stem wood over a rotation period (Pettersson, 1955). However, the economic merits of such a system were debated

(Pettersson, 1951). In Sweden, a broader thinning discussion, both biologically and economically, evolved in first decades of the 20th century (Andersson, 1911; Carbonnier, 1936) and Anderssson (1911) seems to have been the first Swedish forester to have discussed thinning in terms not only of volume production, but also in terms of "rentability" as formulated by Faustmann (1849) and Preßler, 1860, and previously discussed by Reventlow in a Danish context (although his main thesis were not published until 1879; Reventlow, 1879).

Since reforestation of clear-felled areas in the 19th century was largely dependent on natural regeneration under seed trees, direct seeding or planting was commenced on a very small proportion of the total forest area (Juhlin Dannfelt, 1959). However, interest in seeding and planting increased in southern and central Sweden during the second half of the 19th century (Thelaus, 1882; Kinman, 1907; Kardell, 1997) and this increased interest, and practical experience of, seeding and planting, raised discussions about its profitability (Wallmo, 1897). Wallmo (1897) advocated transformation of even-aged plantations back to uneven-aged stands by continuous thinning from above and an immediate cessation of clear-cutting in areas that had not been cut yet. With roots back in the 19th century, there was a fierce debate between foresters advocating single-tree selection systems and others promoting the clear-cutting system throughout the first half of the 20th century (Wallmo, 1897, 1910, Welander, 1910; Welander, 1940; Öckerman, 1996). Furthermore, even amongst those who advocated use of even-aged plantations there were intense discussions about the optimal thinning method (Schotte, 1912).

Thanks to the newly established Forestry Boards and the Forestry Act of 1903, interest in planting and seeding on private forest land increased in Sweden during the early decades of the last century, culminating in approximately forty thousand hectares per year being planted/seeded in the 1920s (Carbonnier, 1978; Enander, 2001). In the following 20 years, when economic conditions were less favourable, interest in the ideas of Wallmo (1897) increased and seeding and planting was reduced (Carbonnier, 1978). This was not due to definitive proof of the superiority of single-tree-selection cutting but to the severe economic depression in the 1930s. Selective cuttings increased during the Second World War and the increased demand for energy resources from the forest led to increased thinning activity in private forests (Enander, 2001). The decreased interest in even-aged plantations on private land in the south was matched by a similar decline on state-owned land in both southern and northern Sweden (Holmgren, 1950; Carbonnier, 1978). There was a belief that the situation in northern Sweden in the 1930s (large proportions of stands with uneven age class distributions and old stands with low amounts of standing volume and low productivity) would lead to a shortage of raw material for industrial consumers in the near future (Holmgren, 1933). Therefore, research was initiated about the growth reactions of old spruce stands (Näslund, 1942), and the need for thinning of younger stands, both to provide raw material and to reduce rotation periods, was discussed (Holmgren, 1933).

The battle between believers in clear-cutting systems with even-aged plantations and those favouring selective cutting with uneven-aged stands came to an abrupt end in the beginning of 1950s. The single-tree selection system was prohibited in the state-owned forests and to a large extent was also abandoned on private forest land (Nilsson, 2001), following similar developments in Finland some years earlier (Lähde *et al*., 2002). Although the most intensive debates about forestry concerned problems in northern Sweden and early trials with mechanisation of forestry work commenced in this area (Streyffert, 1959), the changes in northern Sweden were followed by similar changes in the south (Carbonnier, 1978). The prohibition of selective cuttings in favour of even-aged plantations, together with mechanisation of forestry work, were the most significant changes for thinning activities in the second half of the last century.

The level of mechanisation in forestry increased rapidly after the Second World War (Leijonhufvud, 1960). Transport from the forests to the industrial consumers had previously been dependent on horse and man power in the first steps and thereafter on railways or rivers. Furthermore, increasing salaries for forestry workers from the mid-1930s (Streyffert, 1959) demanded an increasing level of mechanisation. During the 1930s, 1940s and 1950s the road network increased substantially and trucks took over the transport from the rivers and lakes (Sjöstedt, 1959; Sundberg, 1959, 1978). The chain saw took over from the hand saw during the 1950s and in the 1960s forest tractors (forwarders) took over most of the work previously carried out with horses (Embertsén, 1976; Sundberg, 1978).

Since the machinery introduced for cutting and timber transportation was not economically viable for handling timber of small dimensions (Streyffert, 1959) the mechanisation favoured clear-cutting over thinning (Nordlund, 1996) and this, combined with decreased confidence in the future economic profitability of forestry, prompted a sharp decline in the annually thinned area during the 1960s and early 1970s (Nilsson, 1974). The economic projections changed later in the 1970s and for a period a quarter of the annually thinned area was in stands mature enough for clear cutting (Olsson, 1986).

The machinery introduced for thinning of stands had negative effects on the biological results of thinning. The problems and opportunities associated with mechanisation of the thinnings were analysed and discussed. Studies were initiated about thinning injuries on remaining trees, damage to the ground and related production losses, and on growth and quality following row thinning (Bengtsson, 1955; Carlsson, 1959; Ågren, 1968, Andersson, 1968; Nilsson & Hyppel, 1968; Hedén, 1970; Kardell & Pettersson, 1973; Fries, 1976). However, although the importance of these biological problems was acknowledged, the mechanisation of thinning was essential for economic reasons, and mechanisation had substantial effects on productivity in forestry during the period 1950-1990. The productivity, in terms of cubic metres harvested per day work, was 1.4 m^3 in 1950 and 10.6 m^3 forty years later (Fryk, 1990). From the beginning of 1990^{th} and onwards the mechanisation of forestry work has been almost 100% and harvester and forwarders dominates both clear cutting as well as thinning operations (Anon. 1991; Nordlund, 1996). The introduction of the single-grip harvester in Sweden, approximately twenty years ago, drastically changed the profitability of thinnings. From then and onwards it has been possible to get a net income even in the first thinning.

Impact of initial spacing on stem volume production, tree properties and profitability

Growth of individual trees and volume production per area

Changes in economic conditions in Sweden, including reductions in timber prices and increases in labour costs during the 1960s and 1970s, led to planting at wider spacings (Anon., 1969; Nilsson, 1978). General reductions in the numbers of seedlings planted per hectare in afforestation and reforestation activities in the second half of the 20th century also occurred in other parts of Europe (Burschel, 1981; Kenk, 1990; Kairiūkštis & Malinauskas, 2001; Øyen, Øen & Skatter, 2001). Understanding growth and wood quality responses of trees in stands planted at different initial densities is crucial for sound economic decisions, and the ideal initial spacing depends on a combination of ecological, economic and technical factors.

Diameter

Spacing experiments have consistently shown that breast height diameter increases with increases in initial spacing. Between-tree differences in diameter growth emerge when the trees start to compete for light, water and nutrients (Nilsson, 1993) and increase up to the time when the canopy closes (Sjolte-Jørgensen, 1967; Zhang *et al*., 2002). For instance, Lynch (1980), found no significant differences in diameter growth up to six metres stand height. The mean diameter of the trees in a stand up to the time of first thinning is linearly related to the initial spacing (Vanselow, 1942, 1950, 1956; Wiksten, 1965; Haveraaen, 1981; Handler & Jakobsen, 1986; Orlic, 1987). At very wide initial spacings (> 3m), the trees develop essentially as openly grown trees, with no further increase in diameter growth with further increase in initial spacing, as shown for Norway spruce, Lodgepole pine and Western white pine by Handler & Jacobsen (1986), Cochran & Dahms (1998) and Bishaw, DeBell & Harrington (2003), respectively. The differences in mean diameter established by the time of canopy closure are largely conserved for the rest of the rotation period, provided that the thinning regime applied does not interfere with the trees' growth (Sjolte-Jørgensen, 1967). This implies that relative between-spacing differences in diameter in the early development phase decreases with time (Vanselow, 1956; Harms, Whitesell & DeBell, 2000).

Height

For Norway spruce, the mean height is lower in stands with high initial planting densities than in sparser stands (Wiksten, 1965; Orlic, 1987; Kairiūkštis & Malinauskas, 2001; Øyen, Øen & Skatter, 2001), because the differentiation among tree classes is greater, and the percentage of suppressed trees is higher in dense plantations (Sjolte-Jørgensen, 1967; Haveraaen, 1981; Handler & Jakobsen, 1986). However, initial spacing seems to have very little influence on growth in top height except in very dense or very sparse stands (Hamilton & Christie, 1974; Braastad, 1979; Haveraaen, 1981; Handler & Jacobsen, 1986; Spellmann & Brokate, 1991; Pettersson, 1992). On poor soils in harsh climate in northern

Sweden it has been found that the top height increases with increasing spacing (Nilsson, 1994).

Stem form

There is a strong correlation between tree size and tree form; the larger a tree's DBH at a given height, the lower the form factor. Thus, the low form factors (or strong taper) reportedly associated with sparsely populated stands (Kjersgård, 1964; Hamilton & Christie, 1974; Handler, 1990) are to a large extent caused by differences in tree diameter (Nylinder, 1958; Kairiūkštis & Malinauskas, 2001).

Volume

Numerous studies on both Norway spruce (Braathe, 1952; Klem, 1952; Kjersgård, 1964; Wiksten, 1965; Braastad, 1979; Haveraaen, 1981; Handler & Jakobsen, 1986; Handler 1988, 1990; Johansson, 1992; Pettersson, 1992; Johansson & Pettersson, 1996; Øyen, Øen & Skatter, 2001) and other species (Eklund, 1956; Lynch, 1980; Kilpatrick, Sandersson & Savill, 1981; Tuyll & Kramer, 1981; Cochran & Dahms, 1998; Neilsen & Gerrand, 1999) in which the effects of initial spacing have been examined have consistently found that the stem volume production per hectare is lower, while the diameter growth of the individual trees is enhanced, in widely spaced stands.

In Sweden, the effect of initial spacing on stem volume production in Norway spruce stands has been investigated by several authors (Wiksten, 1965; Eriksson, 1976; Johansson, 1992; Pettersson, 1992, Johansson & Pettersson, 1996).
Like diameter growth, much of the difference in volume production between different initial spacings is established early in the rotation and differences in current annual stem volume production between different spacings are small after stand closure and the differences in total production between sparse and dense plantations diminish with time (Sjolte-Jørgensen, 1967; Handler & Jakobsen, 1986; Handler, 1988). Most of the stands examined by Pettersson (1992) had initial square spacings between 1 and 2.5 m, but stands at 0.75 and 3 m spacings were also represented. The reduction in volume production associated with increases in initial spacing were found to be minor at densities larger then 2500 stems per hectare, but to be substantial at densities less then 1000 stems per hectare. Pettersson (1992) found that production was 36 m^3 (36%) lower with 3 m than with 2 m initial square spacing at 10 m stand top height. At 14 m stand top height the corresponding difference was 77 m^3 or 28%. A similar curvilinear relationship between spacing and volume production to that described by Pettersson (1992) was also found in a 24-year-old spacing experiment in Germany reported by Spellmann & Schmidt (2003). The total volume production with a 5 x 5 m spacing was approximately half the production with 2.5 m square spacing (115 m^3 and 213 m^3, respectively), while the corresponding difference between 2.5 m square spacing and 2.5 x 1.25 spacing was only 39 m^3. Further effects reported by Pettersson (1992) were that height differentiation was lower, and the diameter distributions were more skewed towards lower diameters in denser stands. In addition, several authors (Kjersgård, 1964; Handler & Jakobsen, 1986; Spellmann & Schmidt, 2003) have claimed that most of the extra volume produced in stands

with narrow spacing is in small diameter classes. During a whole rotation, Eriksson (1976) estimated that the production reductions associated with increasing spacing from 1 m to 3 m results in reductions of volume production by 40-80 m^3sk, depending on the site index. The stands with 3 m spacing were also poorly represented in the material Eriksson examined. Johansson (1992) found that increasing the initial spacing from 1.5 to 2.5 m in 31-year-old stands on fertile sites in south-west Sweden (estimated dominant height at 100 years = 36 m) led to a reduction in volume production of 42 m^3 or 13%, over the rotation.

The total stem volume production and total above-ground standing biomass was also examined by Johansson & Pettersson (1996) in a 43-year-old spacing experiment on some of the most fertile sites in southern Sweden (estimated dominant height at 100 years = 35-38 m), thinned four times with equalised cutting (leaving the same basal area in the stand after thinning, independently of basal area in each different spacing regime before thinning). The growth losses in stands with 2.5 m spacing compared to stands with 1.5 and 1.0 m spacing amounted to approximately 100-120 m^3, or 15%. Differences between stands with 2.5 and 2 m initial spacing amounted to approximately 80 m^3. Due to the equalised cutting the differences in standing above-ground biomass were insignificant, but the results indicated a weak tendency for branch proportions of the trees to increase with increased initial spacing.

Influence of initial spacing on individual tree properties

Quality could be defined as: the totality of features and characteristics of a product or service that bear on its ability to satisfy stated or implied needs. Although quality, according to this definition, could mean almost anything, there has been a strong general consensus regarding key quality parameters – and trees with large straight stems, small knots and low percentages of juvenile wood (narrow innermost year rings) have fetched higher prices than those with the opposite characteristics – for a long time. The main products made from Norway spruce wood in Sweden are timber for construction, pulp, paper and bio-energy. The ways to improve economic returns from the forest are to increase yields, reduce production costs and/or increase the value of the produced wood.

An increasing proportion of the forest resource is being transformed from naturally generated stands to fast-growing planted stands (Kennedy, 1995; Perstorper *et al*., 1995) and the trees produced in those plantations will have significantly lower quality (Johansson, 1997). Although numerous authors, considering various tree species, have claimed that the largest disparity in wood quality associated with different methods of regeneration are attributable to differences between planting and natural regeneration rather than to differences between various planting distances (Johansson, 1997; Agestam, Ekö & Johansson, 1998; Lindström, 2002; Zhang *et al*., 2002) an increase in initial planting distance will further decrease the wood quality (Persson, 1985; Høibø, 1991a; Johansson, 1997). In a study by Klang (2000a), dense natural generated Norway spruce stands were re-spaced (at 1-2 m height) to the same spacing as planted stands (same genetic origin) and compared for growth and wood quality after 31-34 years. The mean annual increment (excluding seed trees) was 26% lower in the re-spaced stands but fewer trees suffered defects such as spike knots, sharp bends and forked stems. Small and in-significant differences were found for diameter of the thickest branch, stem straightness, average annual ring width and basic density.

One of the most important quality aspects of a tree is its diameter at breast height (MacDonald & Hubert 2002), because larger trees fetch higher prices per cubic metre and they are less expensive to cut (Tufts & Binker, 1993; Brunberg, 1997; Tufts, 1997; Eliasson & Lageson, 1999; Nurminen, Korpunen & Uusitalo, 2006). As stated in previous section, spacing experiments have consistently found diameter at breast height to increase with increased spacing.

Density

Tree properties in Norway spruce are under strong genetic control (Rozenberg & Cahalan, 1997; Hannrup *et al*., 2004) but it is important to remember that anything that affects the physiological performance of a tree, and hence its growth, may also affect its wood properties. Wood properties, such as basic density, wood structure, juvenile wood content and length and size of branches are all related to crown development and growth (Lindström, 1996a, 1996b; Deleuze *et al*., 1996) and thus affected by initial spacing (Johansson, 1997; Mäkinen & Hein, 2006) as well as subsequent thinning regime (Bergstedt & Jørgensen, 1997; Pape, 1999a).

Latewood percentage in coniferous decreases with increases in growth rate (Nylinder, 1951; Brazier 1980; Cregg, Dougherty & Hennessey, 1988), and since the latewood percentage is strongly correlated to basic density (Olesen, 1976; Mäkinen, Saranpää & Linder, 2002), increased annual ring width is negatively correlated with basic density (Nylinder, 1953; Eriksson, 1966; Olesen, 1976; Moltesen, Madsen & Olesen, 1985; Lindström, 1996b; Dutilleul, Herman & Avella-Shaw, 1998; Pape, 1999b). Wood density (as a mean value in the stand) tends to decrease with wider initial spacing (Klem, 1952; Persson, 1975a; Johansson, 1993; Johansson & Pettersson, 1996; Zhang *et al*., 2002) even though trees with identical size, in most cases, had similar density independent of spacing (Anon, 1960; Johansson, 1997).

Juvenile wood

The so-called juvenile or core wood in the annual rings closest to the pith has different properties from mature wood (*e.g.* Boutelje, 1968; Bendtsen, 1978; Saranpää, 1994). Compared to mature wood, it generally has low basic density, thinner cell walls, larger cell lumens, shorter tracheids, low cellulose contents, high lignin contents, large microfibrillar angles and increased spiral grain (Zobel & Sprague 1998). Most of those features are considered undesirable for both paper and sawn timber production (Danborg, 1994a; Brolin, Norén & Ståhl, 1995; Perstorper *et al*., 1995; Forsberg & Warensjö, 2001). The quality of sawn goods may be low if they contain both juvenile and mature wood (Saranpää, 1994). Each of these properties gradually changes with increasing age and thus the boundary between juvenile and mature wood is not sharp (Harris, 1981; Zobel & Sprague, 1998; Lindström, 2002). In Norway spruce these gradual changes occur in the 5-

25 innermost year rings (Boutelje, 1968; Saranpää, 1994; Kliger *et al*., 1995), while according to a literature review published by Lindström (2002), much of the wood maturation in Norway spruce takes place in the first 10 growth rings. Increased growth at young ages will increase the percentage of juvenile wood in the bottom log at a given final diameter (Yang & Hazenberg, 1994; Lindström, 2002; Zhang *et al*., 2002). In an investigation of the effects of spacing on ring numbers of juvenile wood in two other species of *Picea*, Yang (1994) found no significant difference in this variable between *P. mariana* trees with square spacings of 1.8-2.7 and 3.6 m, but there was a significant difference in *P. glauca* stands; those with the wider spacing having 3-4 more juvenile wood rings than stands with the closer spacing.

Increased growth rate, either by increased initial spacing or subsequent thinning at any time in a tree's life, will increase the amount of juvenile wood at some position along the stem. To minimize the amount of juvenile wood for a given amount of stem volume per hectare in the final cut (assuming the site index to be constant and the thinnings applied to have no selection effect) the diameter growth rate should be low when the height growth is high, and since height growth peaks early in the rotation period (Assmann, 1970) a dense young stand should become less dense with increasing age. In addition, the most valuable part of tree, the bottom log, should have a low percentage of juvenile wood if the initial density is high, the growth rate is enhanced as much as possible in the thinning phase and the rotation period is prolonged (Danborg, 1994a; Pape, 1999a; Lindström, 2002).

Branch size and number

Both for Norway spruce and other species, the diameter of the largest knot in the bottom log is one of the most important quality parameters for timber (*e.g.* Kramer, Dong & Rusack, 1971; Persson 1977, Todoroki, West & Knowles, 2001). There are numerous national systems for grading the quality of both standing timber and sawn goods. Historically, in the best quality trees in Norway spruce, the largest dry knots should not exceed 20 mm under bark at 5 m stem height (Abetz & Merkel, 1968; Dumm, 1971; Kramer, Dong & Rusack, 1971; Andersson, 1974).

Branches live longer in sparse plantations (Merkel, 1967; Johansson, 1992) and growth rates of branches; as long as they are vital, follow those of the stem (Eklund & Huss, 1946; Nylinder, 1958; Shinozaki *et al*., 1964; Braastad, 1979; Vestøl, Colin & Loubére, 1999). The trees in sparse stands tend to fill the gaps by expanding their branches, and since branch length in the upper crown with healthy developing buds, independent of tree species, is linearly positively correlated to branch diameter (Cannell, Morgan & Murray, 1988; Baldwin *et al*., 2000; Fernández & Noreo, 2006) branch size tends to increase with reductions in initial spacing or with increasing thinning grade. The diameter of the largest branch in the bottom log of Norway spruce is inversely linearly related to stand density (*e.g.* Kramer, Dong & Rusack, 1971; Handler & Jakobsen, 1986; Spellmann & Brokate, 1991). In the first and second logs of both Sitka and Norway spruce trees, it has been reported that branch size increases upwards along the stem (Merkel, 1967;

Brazier & Mobbs, 1993; Kairiūkštis & Malinauskas, 2001; Mäkinen & Hein, 2006), especially if thinning has been carried out (Abetz & Merkel, 1968; Abetz & Unfried, 1983). Thus, the height to the first living branch, which decreases with increasing initial spacing (Handler & Jakobsen, 1986), is an important quality parameter at the time of first thinning. The branches in the bottom log will increase in size if thinning is carried out at early ages as reported for both Norway spruce (Madsen, Moltesen & Olesen, 1978; Braastad & Tveite, 2000; Spellmann & Schmidt, 2003), and Scots pine (Uri, 1998; Fahlvik, Ekö & Pettersson, 2005a). The total number of branches seems to be only moderately affected by initial spacing (Nylinder, 1958; Moltesen, Madsen & Olesen, 1985; Handler & Jakobsen, 1986; Klang, 2000a).

Stem straightness, compression wood and stem cracks

The quality and yield of sawn wood is strongly influenced by the straightness of the tree (Zobel & van Buijtenen, 1989). Increasing the initial spacing increases the absolute bow height in the bottom log of Norway spruce trees (Høibø, 1991b). Kairiūkštis & Malinauskas (2001) reported that stem straightness increases with increases in planting density up to 12500 stems per hectare. However, Johansson (1992) found no statistically significant correlation between spacing and crookedness in Norway spruce. In Scots pine, increased proportions of straight trees with decreased initial spacing have been reported by Prescher & Ståhl (1986) and Agestam *et al.* (1998). Brazier & Mobbs (1993) found correlations between the poorer structural performance of logs from widely spaced plantations with decreased stem straightness, and increases in the size and number of knots and the amount of juvenile wood. In addition, leaning and crookedness in trees lead to an increase in the extent of compression wood (Brazier, 1977; Rune & Warensjö, 2002).

It has been shown that high growth rates in Norway spruce, in combination with drought, can lead to stem cracks (Rognerud & Haveraaen, 1984; Persson 1985, 1994; Grabner *et al.*, 2006; Rössler, 2006). In a 24-year-old spacing experiment with Norway spruce in Denmark the percentage of trees with stem cracks was around 15% with 3 m spacing while the corresponding figure for 2 m spacing was approximately 3% (Persson, 1985).

Final remarks

Large knots, high juvenile wood contents and low basic density are all correlated to low structural performance of sawn wood (Shivnaraine & Smith, 1990; Kliger *et al.*, 1995; Norén & Persson, 1997), therefore the structural performance of wood tends to be low when it originates from trees that have grown rapidly because the site is fertile, the initial spacing is wide, they are intensively thinned or a combination of those variables (Schaible & Gawn, 1989; Brazier & Mobbs, 1993; Danborg, 1994a; Kyrkjeeide, Lindström & Thörnqvist, 1994; Kliger *et al.*, 1995; Norén & Persson, 1997).

Scope to influence timber quality by cleaning, thinning or use of shelter in stands with different initial spacings

In a stand, regardless of initial spacing, there are large variations in the breast height diameter of the individual trees. The mean diameter is strongly affected by initial spacing but not the kurtosis or skewness of the distribution (Vanselow, 1942, 1950, 1956; Johansson, 1992; Pettersson, 1992). Therefore, it is interesting to know whether some undesirable wood properties related to wider spacings are linked solely to the increased growth rate of individual trees or if the spacing *per se* also has an effect (Persson, 1975a; Johansson, 1992; Moberg, 1999). For some properties the additional effect of spacing *per se* is minor, for example the diameter of the largest knot in the bottom log (Johansson, 1992; Vestøl, Colin & Loubére, 1999; Kairiūkštis & Malinauskas, 2001) and basic density (Persson, 1975a; Johansson, 1993). For other properties, such as knot content, the spacing effect is more important (Persson, 1975a, Johansson, 1997).

For properties that are strongly correlated to DBH, for example the diameter of the largest knot, the mean quality in the stand could be enhanced by thinning from above (Nordberg & Olsson, 1987; Høibø, 1991a; Eriksson, 1990, 1992). Pape (1999c), found that thinning from above increased the mean basic density in the stand compared to thinning from below with the same thinning grade and intensity. However, there are large between-tree variations in each quality trait at each particular spacing (Høibø, 1991b; Klang & Ekö, 2000). Therefore, trees with undesirable properties should be cut in thinning independently of diameter (Norén & Persson, 1997; Klang, Agestam & Ekö, 2000), and a spacing recommendation to promote a certain timber quality might change for either wider or closer spacing if other silvicultural "tools" including thinning is taken into consideration (MacDonald & Hubert, 2002, Eriksson, 2004).

As stated above, the largest differences in quality for different methods of regeneration is not between different planting distances but between planting and natural regeneration. It has also been shown that a shelter (high or low) can increase the quality of planted seedlings in a similar way to increased spacing (Klang & Ekö, 1999; Valkonen & Ruuska, 2003). For coniferous species, quality measures such as knot size and lumber strength tend to show sharp changes with differences in spacing, due either to differences in planting distances or pre-commercial thinning, when the density is < 2000-3000 stems per hectare, but changes in spacing will have a minor impact on tree properties and quality when the density is higher (Malinauskas, 2002; Zhang et al., 2002; Fahlvik, Ekö & Pettersson, 2005a).

Plant mortality, advanced regeneration and natural regeneration

In order to identify and attain a desirable plantation density, the initial number of planted seedlings is only one of the factors to consider. Many other factors may cause the establishment of plantations to be sub-optimal, and the initial spacing may either decrease due to mortality (Andersson, 1976; Petersson & Örlander, 2003; Petersson, Örlander & Nilsson, 2004) or increase due to advance regeneration (Tirén, 1949; Andersson, 1988) and subsequent natural regeneration (Pohtila & Valkonen, 1985; Räsänen *et al*., 1985; Ackzell, 1992, 1994; Fällman & Nenzen, 2005). Natural regeneration could contribute to a significant increase in stand density under appropriate management regimes on suitable sites (Kenk, 1990; Ackzell, 1992; Karlsson, Nilsson & Örlander, 2002) but they may also be seen as a problem since they reduce the growth potential of genetically improved planted material (Hägglund, 1983). Additional naturally established seedlings may help to boost volume production, improve quality, spread risks and increase economic returns (Tham, 1988; Lohmander, 1992; Bergqvist, 1999; Valkonen & Valsta; Fällman & Nenzen, 2005; Agestam *et al*., 2006).

Economy

Although economic issues were not directly addressed in the papers underlying this thesis, I believe there is a need for a brief discussion of economic aspects of intensity in reforestation programs.

The optimal planting density is dependent on alternative rate of return ("interest rate"), planting and logging costs, site conditions, volume production, wood quality and other factors (Solberg & Haight, 1991). If planting density is the only silvicultural issue considered (no cleaning or thinning is used before final felling) and the approach presented by Faustmann (1849) is used, knowledge about differences in volume and quality production (including diameter distribution and prices), cutting, hauling and transportation costs, together with an interest rate all need to be known in order to choose an optimal planting density. However, there is a long time lag between decision-making and the final evaluation of the outcome of the decisions. Furthermore, even if we had perfect information about future prices and costs, the chosen planting pattern affects the conditions for future silvicultural decisions regarding, for example, pre-commercial thinning and thinning (Fahlvik, 2005), and those regimes also affect volume production and profitability (Fahlvik, Ekö & Pettersson, 2005). The number of possible silvicultural regimes is almost infinite and very large even if many simplifications and assumptions are made. Another important factor to bear in mind is that even if perfect calculations are made, based on perfect information, the resulting decisions may significantly affect future conditions if applied on a large scale.

Nevertheless, it is important to use net-present-value calculations as a tool (among others), while bearing in mind that they are simplifications. If quality aspects are taken into consideration than the optimal density in the young stand increases (Hyytiäinen, Tahvonen & Valsta, 2005). For various places, times and species, a number of authors have claimed that it would be economically preferable to decrease the planting density compared to common practice (Häägg, 1921; Oksbjerg, 1960; Andersson, 1963; Hannelius, 1978; Lohmander, 1994; Gong, 1998; Zhou, 1999, Eriksson, 1999; Soalleiro, Gonzalez & Schröder, 2000). Generally, high interest rates are associated with low initial spacings and low initial spacing is also preferable at low site indices (Hannelius, 1978; Söderström, 1980; Solberg & Haight, 1991; Zhou, 1999).). It is important to consider economic aspects throughout the whole rotation in the regeneration phase and identify a regeneration method that exploits natural regeneration (Wieslander, 1986; Fällman & Nenzen, 2005).

Impact of thinning on stem volume production, individual tree properties and profitability

Initial growth responses of individual trees to thinning

The diameter of a tree that competes with its neighbours for any growth resources will generally increase more if some of those neighbours are removed by cutting than if they are not, and the more intense the cutting the stronger the diameter growth response of the remaining trees will generally be.

Diameter growth and growth of the largest trees in the stand

Although thinning experiments have consistently found thinning from below to increase the mean diameter growth of the remaining trees in the stand there has been some debate about the response to thinning of the largest trees (Braastad & Eikeland, 1986; Braastad, 2001; Mäkinen & Isomäki, 2004a). In Norway, Braastad & Tveite (2001), found that the difference in mean diameter of the 800 largest trees in intensively thinned stands and unthinned stands after 25 years of observation was only 1.2 cm. In the cited Norwegian report the various thinning grades and intensities were measured as mean values over time of the distance between the remaining trees in relation to top height, and thus comparison of the thinning program applied to those applied in other experiments is not straightforward. Generally, however, the thinning programs in the cited study appear to have been rather light, and the reductions in stem numbers compared to the unthinned controls never exceeded 50%. Light thinnings have been reported to have a minor influence even on the largest 100-200 largest stems per hectare (Slodičák & Novák, 2003). After more than 35 years of observation, Johansson & Karlsson (2004) found that the 100 to 400 largest trees in stands repeatedly thinned lightly from below showed a diameter increase of 3.1 cm to 3.8 cm compared to corresponding trees in unthinned control plots. A single heavy thinning from below with the removal of 57% of the basal area yielded similar increases, of 3.0-4.2 cm. In a similar, but more long-term experiment Karlsson (2006) found that after a 35 year observation period repeated thinnings from below resulted in the 100 and 400 largest trees being 5.2 and 4.5 cm larger than those in unthinned control stands, respectively. A single heavy thinning from below with the removal of approximately 70% of the basal area resulted in additional increases in the diameter at breast height of the 100 and 400 largest trees of 7.1 cm and 8.2 cm, respectively. In the treatment with a single heavy thinning from below the differences in tree dimension are to a large extent caused by the growth reaction in the first 10-15 years. The mean growth reaction of the 100 largest trees during the initial seven years after thinning compared to unthinned controls was 5.7 mm per year (Karlsson, 2006). Positive growth responses of the largest trees in Norway spruce stands following thinning from below have also been reported by Hamilton (1976), Abetz & Unfried (1984), Spellmann (1986), Abetz & Feinauer (1987), Kramer & Holodynski (1989), Mäkinen & Isomäki (2004a), Herbstritt (2006), Rössler (2006), Skovsgaard

(2006) and Slodicak & Novak (2006) (see also table 4 in Paper III) and in stands of other tree species by (*inter alia*) Mitscherlich (1981), Medhurst, Beadle & Neilsen (2001), Mäkinen & Isomäki (2004b), Rytter & Stener (2005) and Zhang & Oliver (2006).

Diameter distribution

In addition to knowledge about the response of diameter growth after thinning, the stem size distribution of the trees is an important determinant of the commercial value of a given volume of timber. The potential end use of trees is dependent on stem size (Grøn, 1940; Stevens & Barbour, 2000) but certainly also on other features, so prices vary for trees with different diameters. Norway spruce timber is better paid per cubic metre for larger top diameters up to an asymptotic level and above a certain diameter the price per cubic metre decreases. This implies that, for a silviculture regime aiming for clear-cutting, a thinning program that narrows the diameter distribution will be economically advantageous since a higher percentage of the total volume could be cut at optimum price (Hyytiäinen, Tahvonen & Valsta, 2005). Generally, the shape of the diameter distribution curve in the stand before thinning is not strongly dependent on initial spacing, which, as argued in a previous section, affects the mean diameter, but not the kurtosis or skewness of the distribution (Vanselow, 1942, 1950, 1956; Johansson, 1992; Pettersson, 1992).

The diameter distribution of trees in a stand is most strongly affected by the thinning programme (Karlsson & Norell, 2005a; Slodicak & Novak, 2006), the higher thinning grade and intensity, the higher the proportion of the total volume in larger diameter classes (Henriksen, 1961; Hamilton, 1976; Bryndum, 1978).
For different thinning programmes in Norway spruce, Karlsson & Norell (2005b) found that, in the long run, it was difficult to narrow the diameter distribution by thinning, even though the diameter range is tightened directly after each thinning from either above or below. However, Danish experiments in Norway spruce stands reported by Bryndum (1974, 1978) show that it is possible to narrow the diameter distribution with a frequent thinning schedule. The thinning program in the studies by Bryndum (1974, 1978) was more flexible and there were more thinnings than in the experiment reported by Karlsson & Norell (2005b).

Height growth

Independent of tree species, initial spacing and thinning generally has stronger effect on diameter growth than height growth (Braathe, 1952; Sjolte-Jørgensen, 1967; Hägglund, 1972; Hamilton, 1981; Lanner, 1985; Huss, 1988; Sharma, Burkhart & Amateis, 2002). However, it has been shown that height growth in Norway spruce may increase following respacing in very dense stands (Näslund, 1935; Eklund, 1952; Chroust, 1969). The thinning effect on height growth development could be rather confusing if mean stand heights are compared at different periods since the time courses of effects of the thinning method applied (mainly thinning from below) will depend on the thinning intensity (Eide & Langsæter, 1941; Bryndum, 1969, 1978). The real thinning effect on height growth should be measured on the same individual trees at each revision. Most long-term studies of thinning in Norway spruce stands have found it to have insignificant effects on increase in top height (Bryndum, 1978; Huss, 1990; Kuliešis & Saladis, 1998; Laasasenaho & Koivuniemi, 1990; Mäkinen & Isomäki, 2004c). Forty-four years after the establishment of a Norway spruce experiment in Scotland in which thinning with three different thinning grades (B, C and D), replicated four times were applied, Hamilton (1976) found significant differences in top height growth. The D-thinning grade resulted in a 10% increase in top height compared to the B-grade, and the C-grade yielded intermediate values. Similar results have been reported by Bryndum (1969), who found a 12% increase in top height following D-grade compared to B-grade thinning after 31 years of observation. However, reduced top height growth after heavy thinning has been reported by Abetz (1976) and Abetz & Unfried (1984). Thinning is reported to decrease the initial height growth (in the first 5-10 years) in Scots pine (Valinger, 1992a), loblolly pine (Yu *et al*., 2003), lodgepole pine (Brockley, 2005) and red alder (Hibbs, Emmingham & Bondi, 1989). It has been reported that top height growth of spruce and other tree species declines in the first years following thinning, recovers, and then finally exceeds growth in corresponding unthinned stands (Näslund, 1942; Harrington & Reukema, 1983; Eriksson & Karlsson, 1997; Mitchell, 2000; Valinger, Elfving & Mörling, 2000; Sharma *et al*., 2006). Thus, differences in the length of the observation period following thinning in different investigations may explain, to some extent, differences in reported effects of thinning on height growth and increase in top height.

Stem form

Volumes estimations of standing forest timber for sale in the last part of the 19th century were inaccurate, the resulting estimates were consistently too low (Jonsson 1910) and to meet demands for more fair and accurate estimates of timber sales, more knowledge about the stem form of trees was required and intensively discussed (Pettersson, 1925; Jonsson 1927). For Swedish conditions, useful volume functions for practical forestry and research applications were developed by Näslund (1940, 1947) and further refined by Brandel (1990). The accuracy of the volume functions developed by Näslund for estimates of volume production in thinning experiments was evaluated by Karlsson (1997), who concluded that the functions by Näslund overestimated the volume production in unthinned stands.

The reason for the problems outlined above in converting DBH and height growth to stem volume is related to the stem form of the trees and its changes over time due to forestry practices (Myers, 1963; LeBlanc, 1990; Mäkinen, Nöjd & Isomäki, 2002). Estimates of thinning or spacing responses may be misleading if only changes in DBH are taken into consideration (Jonsson, 1910; Curtis, Marshall & Bell, 1997; Tasissa & Burkhart, 1997). Stem form also influences the yield of sawn timber (Eklund, 1949; Baltrušaitis & Pranckevičienė, 2001).

The form of a tree is closely related to its crown parameters (Larson, 1963; Fayle & MacDonald, 1977; Dean, 2004) and the forces applied by winds to the crown (Jonsson, 1912; Valinger, 1992b; Jakobsson & Elfving, 2004). Therefore, the ring width in young stands, with living branches close to the ground, are likely to be maximal in the lower parts of the trees' stems (Farrar, 1961). As trees in a stand grow they gradually compete increasingly stronger with each other (Nilsson & Gemmel, 1993; Skovsgaard, 1997) and consequently the trees' crowns gradually rise (Kramer, 1966; Kantola & Mäkelä, 2004; Mäkinen & Isomäki, 2004a) and the point along the bole where the growth rate in ring width is maximal gradually shifts upwards (Farrar, 1961; Reukema, 1961).

After thinning, increased wind exposure of the lower part of the crown combined with increases in crown width after release and reductions in the mutual support from neighbouring trees makes the remaining trees more vulnerable to wind damage (Persson, 1975b; Nielsen, 2001) and in adaptive responses to this new situation a higher amount of growth resources are located in basal stem parts (Valinger, 1992b; Mitchell, 2000; Nielsen 2001, Holgén, Söderberg & Hånell, 2003; Nielsen & Knudsen, 2004) and/or coarse roots (Jacobs, 1936, 1954; Pryor, 1937; Johansson, 1941; Eklund, 1952; Urban, Lieffers & MacDonald, 1994). Changes in stem form have also been related to water and nutrient availability, since increased amounts of water, and reductions in the amount of available nitrogen in the soil tend to improve stand form (Larson, 1963; Mead & Tamm, 1988; Wiklund, Konôpka & Nilsson, 1995). Increases in stem taper (or reductions in form factor) after thinning have been reported for numerous species by many researchers (Bornebusch, 1933; Hagberg, 1942; Vuokila, 1960a; Farrar, 1961; Larson, 1963, 1965; Bryndum, 1969; Barbour, Bailey & Cook, 1992; Mitchell, 2000; Peltola *et al.*, 2002), but the priority of growth at the stem base and coarse roots after release gradually declines with time (Myers, 1963; Thomson & Barclay, 1984). Stem form changes after thinning is reported to differ for trees of various social positions (Thomson & Barclay, 1984; Arbaugh & Peterson, 1993).

The crop form factor in the so-called Bowmont Norway spruce thinning experiment showed small differences after 44 years of light, moderate and heavy thinning from below (0.479, 0.478 and 0.461 respectively following B-, C- and D-grade thinning) (Hamilton, 1976). Stem form measured as the taper between bole heights of 1.3 and 6 m has been shown to increase, in both Norway spruce and Scots pine, with increasing release in long-term thinning experiments in Sweden and Finland (Karlsson, 2000; Mäkinen & Isomäki, 2004a, 2004b; Mäkinen, Hynynen & Isomäki, 2005).

In evaluations of the effects of spacing and thinning on stem form it is important to consider that larger trees generally have greater stem taper and hence lower form factors. A comparison of mean values of form or taper in differently treated stands would to a large extent merely be a comparison of the form and taper of trees of different sizes. The treatment effect is more interesting when trees with the same diameter and height subjected to different treatments are compared. In a combined spacing and thinning experiment in loblolly pine stands, Baldwin *et al.* (2000), showed that trees of identical height and diameter had more cylindrical lower boles and increased stem taper in the upper part of their crowns in heavily thinned stands than in unthinned stands. Bryndum (1974, 1978) showed that there were small differences in relative taper for Norway spruce (taper at a given breast height diameter) following different thinning treatments. Henriksen (1961) investigated a Sitka spruce thinning experiment in Denmark and concluded that, "the relative stem form is largely unaffected by the grade of thinning". Norway spruce has been shown to be a less plastic species than, for example, Scots pine (related to differences in shade tolerance) and changes in stem form and branch development due to increased or released competition in the former species are less pronounced than in the latter (Nilsson & Gemmel, 1993).

Impact of thinning regime on stem volume production

Basal area vs. volume production

Before we discuss the effects of different thinning programmes on volume production, there is one important aspect to consider. In 1932, Wiedemann published data from thinning experiments in beech where the basal area growth was higher after heavy thinning than light thinning, but the calculated volume production was unaffected over a large range of remaining basal areas. Later, numerous studies have shown that the basal area response to thinning is higher than the volume growth response (Carbonnier, 1954, 1957; Bryndum 1969, 1974, 1978; Schober, 1979, 1980) and this effect is especially pronounced for short time intervals after heavy thinnings (Carbonnier, 1974; Agestam, 1979; Eriksson, 1987). It could be argued that differences in height growth or changes in stem form could be responsible for these conflicting results. However, Wiedemann (1932) claimed that stem volume growth will always differ between any two stands, even stands with the same basal area growth, height growth and form development. There are numerous ways to calculate volume production in a stand (Karlsson, 1998). One of the more simple approaches is to multiply the stand basal area by the stand mean height and average form factor (Wiedemann, 1951; Carbonnier, 1954; Braathe, 1957; Assmann, 1970; Agestam, 1979) and the formula below explains why a thinned and unthinned stand with the same basal area and height growth and the same change in form factor will (almost certainly) differ in terms of stem volume production.

$$V = BA \times H \times F$$

where: V is volume, BA is basal area, H is height and F is the form factor. The volume growth (ΔV) for a certain time period can then be calculated as V_2-V_1, or as follows:

$$\Delta V = BA \times \Delta FH + FH \times \Delta BA + \Delta FH \times \Delta BA$$

This equation shows that volume growth is not only related to basal area growth but also to the actual amount of standing basal area in the stand. The increase in volume due to the increment in height and increment or deterioration of the form factor is proportional to the standing basal area. Therefore, volume production will differ between a thinned stand and an unthinned stand with the same basal area growth, height growth and changes in form factor. As long as the form-height growth is positive then the differences in basal area growth between the thinned and unthinned stands will be more favourable than the differences in volume growth.

The history of thinning research

Issues concerning stem volume production following different thinning regimes (mostly in Norway spruce and beech) have been studied for more than 100 years. The relevant literature published in the first half of the last century was reviewed by Møller (1952, 1953, 1954), and Braathe (1957) and some of the works they cited still deserve attention from anyone interested in these matters. These studies include papers published by: Schwappach (1911), Wiedemann (1932, 1937, 1951), Vanselow (1943) and Assmann (1950, 1954) for German conditions: Badoux (1936, 1939) and Burger (1951) for Swiss conditions; and Bornebusch (1933), Eide & Langsæter (1941) and Pettersson (1955) for Danish, Norwegian and Swedish conditions. In order to understand the old literature, an introduction to the thinning systems applied, at the respective times and places, is required. Starting in Germany, forestry research institutions were established in various Western European countries, including Sweden in 1902 (Tirén, 1952). Many different ways to characterize a thinning were developed. At an international conference in Mariabrunn in 1903 a program to harmonize the descriptions was adopted. The individual trees were described in detail by their social position, health status and stem quality. The different thinning regimes were initially divided into three main groups: thinning from below (Niederdurchforstung), crown thinning (Hochdurchforstung) and canopy opening (Lichtung). The first of these groups was subsequently divided into three levels or grades; A, B and C. The A-grade served as a control in which only dead, dying or obviously unhealthy trees were cut. The B-grade was a light low thinning and the C-grade a somewhat heavier thinning intended to leave trees with good stem form and well developed crowns with opportunities to expand in all directions. Two different methods of crown thinning or thinning from above were described; light and heavy. Light thinning from above was described as a method for young stands, whereas heavy thinning from above was intended to rapidly enhance the growth of chosen future stems and was seen as a method for older stands (Schotte, 1912).

Later, many experiments also included a heavy or very heavy thinning from below, called D-grade (Bornebusch 1933, Hummel, 1947) and/or various combinations of the grades over time (Carbonnier, 1954). Most experiments carried out according to this system were thinned frequently and lightly. The different thinning grades were usually applied over long time horizon. Since fewer and more intense thinnings are generally applied nowadays, the thinnings applied in those experiments may seem outdated or irrelevant. However, if the mean basal area over time is used for comparison, the old experiments may give valuable knowledge even today.

Assmann (1970) synthesised the result of some of those old experiments and pointed out that for same species on some sites the highest growth of merchantable wood (stem and branches > 7 cm in diameter) would be achieved at a somewhat lower basal area than the highest possible basal area for the stand. Assmann

(1970) called the basal area in the stand that gave the highest basal area production the optimal basal area.

Many of the comparisons in old thinning experiments were marred by inappropriate statistical designs, but Pettersson (1932) solved that problem for the Swedish experiments by using regression analyses (see also Tirén, 1952). Pettersson's analyses focused on volume production solely as a means to facilitate optimal economic decision-making. In two large volumes published in 1955 and 1962 (Barrskogens volymproduktion and Barrskogens värdeproduktion) he concluded that maximum value production demand a more heavy and frequent thinning programme than would be advisable if the sole target was to maximise volume production. The highest amounts of volume production were seen in stands with high basal areas before thinning to which a thinning program with light thinning grades and short time intervals was applied.

In those early days of forest production research, the kinds of statistical designs that we demand today were not applied to the experiments and the thinning practices and methods applied also differed. However, they are valuable because they followed the stand development over long times. Carbonnier (1959), Wiksten (1960) and Fries (1961) examined data obtained in some of those experiments in pine and Carbonnier (1954, 1957) studied some of the spruce thinning plots in southern Sweden.

Zeide (2001) argues that the paradigm regarding the influence of thinning on volume production has shifted several times during the last 250 years. Zeide (2001) and Pretzsch (2004), claims that the opinion of the famous French philosopher Jean Jacques Rousseau (1712-1778) that "All is well when it leaves the hands of the author of all things, everything degenerates in the hands of man" (Rousseau, 1762) was a guiding principle for foresters in their thinning activities during the late 18th century. This view was to some extent revised by Hartig (1795) and Cotta (1828) and the main opinion during the 19th century was that the twin targets of high area production and satisfactory dimensions of the logs in the final cut were best reached by applying late first thinnings and removing low proportions of the basal area in each thinning combined with long rotation periods (Schotte, 1912). However, this silvicultural system was questioned, on economic grounds by the Danish Forester C.D.F. Reventlow (1748-1827) (Oppermann, 1928) in the early 19th century (although his main thesis was not published until 1879 in Danish and 1934 in German). Rewentlow (1879) claimed that volume of individual trees and hence value production per area basis could be enhanced through heavy thinning. The belief in thinning as a tool for increasing volume production increased when early data from newly established thinning experiments started to be published and discussed (Schwappach, 1911; Li, 1923). The observed possibilities to enhance volume production with thinnings together with an aim for larger tree dimensions and shorter rotation implied a movement called "Schnellwuchsbetrieb" (Gerhardt, 1925). The opinion that different types of cuttings could increase production per unit area was strong (Boysen Jensen, 1921) and widely held also in Sweden (Holmerz & Örtenblad, 1886; Wallmo, 1897;

Schotte, 1917, 1921 & 1922a; Ronge, 1928; Holmgren, 1933; Sjöström, 1933; Näslund, 1935).

However, reported data from numerous thinning experiments later showed that the initially positive production per unit area response to thinning later changed to a decrease (Carbonnier, 1957; Holmsgaard, 1958; Wiksten, 1960; Bryndum, 1969). For example, the beech plots investigated by Schwappach (1911) were re-examined by Wiedemann (1932). His conclusions after 50 years of growth differ from those reported after 30 years, and he claimed that volume production is quite similar for mean basal areas between 20 and 40 m^2. On less fertile soils, the growth may be somewhat retarded in denser stands. Furthermore, five years later, Wiedemann (1937) published results from similar experiments in Norway spruce. The volume production responses to different thinning regimes in Norway spruce stands are similar to those in beech stands, and production may be somewhat lower in dense unthinned stands (A-grade) than in lightly thinned (B-grade) stands. Similar results were obtained in a Danish thinning experiment (Bornebusch, 1933) where B- and C-grade thinnings resulted in slightly enhanced production compared to unthinned plots. The small or non-existing differences between different thinning grades combined with the inappropriate statistical design of many experiments led to the results obtained from them being questioned and discussed in the scientific literature (Møller, 1952, 1953; Holmsgaard, 1958).

In the 1930s a new thinning experiment in Norway spruce with more appropriate statistical design, even though, unfortunately, the experiment had no unthinned control plots (B, C and D-grades are represented), was started in Scotland, the so-called Bowmont experiment. The first results concerning volume production in the different thinning regimes from that experiment were published by Hummel (1947) and later by MacKenzie (1962), Hamilton (1976) and Kramer (1978). The highest stem volume production (> 7cm in diameter) was seen in D-grade plots. It could be argued that the differences between the thinning grades in the Bowmont experiment reported by Hummel (1947) could be explained by the use of a 7 cm diameter limit instead of total stem volume. However, even the final examinations of the Bowmont experiment found significant differences between the grades in favour of more intense cuttings (Hamilton, 1976; Kramer, 1978). Furthermore, differences between merchantable volume and total stem volume are greatest at early ages and minor in later stages of a stand's lifetime (Møller, 1933; Ekö, Larsson-Stern & Albrektson, 2004).

Møller (1952, 1953, 1954) and Braathe (1957) summarised the literature about thinning in even-aged stands from the first 50-100 years of organised thinning research and their main conclusion is that it is possible to lower the mean basal area by 50% without any significant decrease in volume production. However, this conclusion has been questioned by Zeide (2001) and Curtis, Marshall & Bell (1997). In long-term thinning experiments in Douglas fir, Curtis, Marshall & Bell (1997) showed that the volume production decreases over the whole range of applied mean basal area levels (approx 11 – 57 m^2/ ha). Curtis, Marshall & Bell (1997) argue that studies in Europe, where similar or even increased volume production has been observed after thinning could be explained to a large extent by inappropriate statistical design, confusions about merchantable and total stem volume production and inappropriate height measurements. The criticisms by Curtis, Marshall & Bell (1997) may be valid to some extent, but the indications that it is possible to increase (or at least not decrease) volume production by thinning are overwhelming and Curtis, Marshall & Bell (1997) misses the most fundamental possibility, that different tree species may differ in their responses to thinning, especially light demanding and shade tolerant species (Roberts, Long & Smith, 1993; Nowak, 1996). The species examined by Curtis, Marshall & Bell (1997) is a shade intolerant species.

Difference in thinning response between pine and spruce (shade-tolerant and shade-intolerant species)

Even though this thesis deals with thinning in Norway spruce stands it is important to clarify differences in growth response to thinning between pine (a shade-intolerant species) and spruce (a shade-tolerant species); the two overwhelmingly dominant tree species in Sweden (Anon., 2006). A majority of thinning experiments in Scots pine in Sweden and Finland have showed that production decreases following active thinning in an intensity-dependent manner (Pettersson, 1955; Carbonnier, 1959; Wiksten, 1960; Fries, 1961; Bucht & Elfving, 1977; Eriksson & Karlsson, 1997; Valinger, Elfving & Mörling, 2000; Mäkinen & Isomäki, 2004d, Mäkinen, Hynynen & Isomäki, 2005). For stands aged 10-50 years, spruce reportedly responds to thinning better than pine according to Judovalkis, Kairiukstis & Vasiliauskas (2005). However, the site indices of most of the material examined in experiments on the responses of pine to thinning have been lower than those of most examined spruce stands, and it has been argued that pine and spruce stands with similar growth rates prior to thinning would have similar reactions to thinning (Jonsson, 1995; Pettersson, 1996). It has been showed, in Danish investigations, that the relative volume growth reduction in actively thinned stands compared to their unthinned counterpart is lower on more fertile sites (Skovsgaard, 1997, 2006). In Norway, the volume growth reduction in thinned compared to unthinned stands is more pronounced (in relative terms) for stands on northern latitudes with low site indices than in more southerly stands with higher site indices (Braastad & Tveite, 2001). Also in Finland, investigations of volume production after thinning with different grades in Norway spruce-dominated stands with low site indices (on peat) have found significant increases in growth reductions with increases in thinning grade, in contrast to stands on more fertile sites (on mineral soil) (Mäkinen & Isomäki, 2004c; Repola, Hökkä & Penttilä, 2006). However, it is still an open question whether the relatively poorer growth response in thinned compared to unthinned stands on less fertile sites is truly a weaker rather than merely a slower response to thinning (Repola, Hökkä & Penttilä, 2006). Pretzsch (2004), reports (in contrast to the discussion above) that Norway spruce has a more positive growth reaction to thinning under poor site conditions. In some thinning experiments in harsh climates with low site indices, the observed growth responses to thinning indicate that production per unit area may be even higher in thinned than in unthinned stands (Langsæter, 1941; Eklund, 1952; Varmola, Salminen & Timonen 2004). Organic nitrogen that was previously tightly bound in the soil may be released after thinning, due to a more favourable micro-climate (Bornebusch, 1930, Nahm *et al*., 2006), and hence increase the production per unit area after thinning (Hesselmann, 1925; Langsæter, 1941; Øyen, 2001).

Effects of different thinning regimes on stem volume production in long-term silvicultural trials in Norway spruce

The majority of the thinning experiments discussed above were conducted in dense stands with short thinning intervals. Nielsen (1990) calls the concept of repeatedly thinning dense young stands (5,000-10,000 stems per hectare) over the whole rotation period, the traditional Norway spruce stand treatment. A new concept for treating Norway spruce stands emerged in Northern Europe in the 1960s involving lower initial spacing (2,500-4,000 stems per hectare), high thinning intensities at young ages and a declining cutting intensity in later stages (Burschel, 1981).

The experiments investigated by, for example, Bornebusch (1933) in Denmark and Carbonnier (1954, 1957) in Sweden represent the traditional stand treatment while the Swedish thinning and fertilization experiment reported by Eriksson & Karlsson (1997) and the Finnish series of thinning experiments reported by Vuokila (1975, 1980) and Mäkinen & Isomäki (2004c) represent the more modern concept. The outcome of different thinning regimes is related not only to the cutting intensities but also to the age of the stands at the start of the experiment (Bryndum, 1964; Carbonnier & Johansson, 1975; Preussler & Schmidt, 1989; Braastad & Tveite, 2001), the number of growing seasons in the comparison (Carbonnier, 1957; Holmsgaard, 1958), the stem number and the basal area before thinning (Pettersson, 1955; Baldwin *et al*., 2000), climate and site index (Skovsgaard, 1997, 2006; Braastad & Tveite, 2001; Pretzsch, 2004). European experiments in even-aged Norway spruce stands subjected to thinning from below are summarized in table 1-3. Even though some of those experiments had been precommercially thinned prior to experiment initiation almost all of them could be regarded as “first” thinnings.

Table 1. Description of thinning experiments.* mean height in stead of top height at start of the experiment

Exp no.	Source	Country	Start of experiment	Age at start (year)	Experimental period (years)	Number of stems stems at start (trees ha^{-1})	Dominant height (m)	Basal area (m^2 ha^{-1})	H100 (m)
1	Bornebush, 1933	Denmark	1910	30	22	5500-7000	8-10*	32-42	26
2	Eide & Langsaeter, 1941	Norway	-	-	-	-	-	-	-
3	Vanselow, 1943	Germany	-	24-48	31-65	4400-5100	-	-	> 35
4	Carbonnier, 1954	Sweden	1906-1927	32-49	25-45	6000-11500	8-13*	33-34	30-36
5	Carbonnier, 1957	Sweden	1906	32	49	2500-4000	11*	38-42	33
6	Bryndum, 1964	Denmark	1910	30	22	5500-7000	8-10*	32-42	26
7	Carbonnier, 1966	Sweden	1940	24	24	-	-	-	32-36
8	Bryndum, 1969	Denmark	1932	41	31	5000-8000	5-7*	17-26	21
9	Bryndum, 1974	Denmark	1933	-	35	7500-8500	12	44	31
10	Carbonnier, 1974	Sweden	1961	35	10	2000-3000	13-14	31-34	32
11	Hamilton, 1976	Great Britian	1930	20	44	4000-5000	8	34-35	38
12	Bryndum, 1978	Denmark	1960	19-27	13	4000-7000	8-10	21-34	38

Table 1 (continued). Description of thinning experiments.* mean height in stead of top height at start of the experiment

Exp no.	Source	Country	Start of experiment	Age at start (year)	Experimental period (years)	Number of stems stems at start (trees ha^{-1})	Dominant height (m)	Basal area (m^2 ha^{-1})	H100 (m)
13	Bryndum, 1978	Denmark	1953	18	20	7000-9000	8-9	21-26	36-38
14	Schober, 1979, 1980	Germany	1896-1929	20-60	40-70	1500-4000	6-21*	-	26-35
15	Braastad & Eikeland, 1986	Norway	1969	28	15	3000-3500	13-14*	35-40	36
16	Eriksson, 1986	Sweden	1906-1927	32-49	55-75	6000-11500	8-13*	33-34	30-36
17	Vesterdal et al., 1995	Denmark	-	-	-	-	-	-	-
18	Bergstedt & Jörgensen, 1997	Denmark	1960	19	32	3000-4500	9-10	21-27	38
19	Eriksson & Karlsson, 1997	southern Sweden	1966-1980	31	25	-	14	-	33
20	Eriksson & Karlsson, 1997	middle Sweden	1966-1980	31	21	-	14	-	33
21	Braastad & Tveite, 2001	Norway	1969-1975	-	25	2000	12	-	34
22	Braastad & Tveite, 2001	Norway	1969-1975	-	25	2000	12	-	26
23	Johansson & Karlsson, 2004	Sweden	1961	35	39	2000-3000	13-14	31-34	32
24	Mäkinen & Isomäki, 2004c	Finland	1961-1981	26-56	13-37	1000-3500	10-24	-	29-36

Table 2. Stem volume production in experimental plots thinned with various grades and intensities in relation to unthinned control. For description of the experiments see Table 1. Extra light thinning = mean periodic basal area compared to unthinned control > 85%, light thinning = 85-75%, normal thinning = 75-65%, heavy thinning = 65-55% and extra heavy thinning < 55% * merchantable volume (> 7 cm diameter)

Exp	Relative production					
no.	Unthinned	extra light	light	normal	heavy	extra heavy
1	100	106	-	110	98	90
2	-	100	96	-	-	-
3*	100	-	103	102	-	-
4	100	-	-	102	-	-
5	100	-	98	96	93	-
6	100	99	-	99	93	93
7	100	-	-	-	90	-
8	100	-	104	101	98	96
9	-	-	100	103	103	-
10	100	104	104	-	-	-
11*	-	100	-	112	111	-
12	100	102	102	100	96	-
13	100	96		104	104	-
14	100	98	95	90	-	-
15	100	-	89	86	-	-
16	100	-	97	97	-	-
17	100	-	98	108	102	-
18	100	108	109	103	105	-
19	100	-	-	94	97	98
20	100	-	-	109	102	81
21	100	99	100	-	105	-
22	100	98	99	-	93	-
23	100	-	99	97	-	-
24	100	99	-	96	95	-

Table 3. Stem volume production during the first period after thinning in experimental plots thinned with various strengths in relation to unthinned control. For description of the experiments see Table 1 and for definition of thinning grades see table 2 * merchantable volume (> 7 cm diameter), ** on heavy single intervention in the young stand with 60-70% basal area removal

Exp	Studied	Relative production					
no.	Period (years)	unthinned	extra light	light	normal	heavy	extra heavy
5	10	100	-	98	108	104	-
8	13	100	113	101	102	107	93
9	11	-	-	100	-	103	-
10	5	100	110	112	-	-	101**
11*	5	-	100	114	118	-	-
12	4	100	101	102	-	-	-
13	8	100	98	107	114	-	-
15	7	100	99		-	-	-
19	6	100	-	106	-	98	80**
20	7	100	-	112	-	93	78**

From the data in table 2 it can be concluded that reduction of the periodic mean basal area level by 50-60% reduces volume production by less than 10% compared to unthinned stands. The "50% rule", that it is possible to reduce the mean periodic basal area by 50%, or do one heavy single intervention in the young stand with removal of half the basal area, without any significant production losses in shade-tolerant species (*e.g.* Møller, 1945, Eriksson & Karlsson, 1997) is also reported for young *Eucalyptus nitens* plantations (Medhurst, Beadle & Neilsen, 2001). Some authors refer to the "50% rule" for net- instead of gross volume production (Oliver, 1988; Zhang, Oliver & Powers, 2005). Common beech, due to its natural ability to occupy space efficiently by vigorous lateral and vertical crown expansion (Pretzsch & Schütze, 2005) might show similar or even better responses to thinning than Norway spruce (Bornebusch, 1944; Bryndum, 1987; Pretzsch, 2003, 2004). Light and moderate thinnings in Norway spruce may even increase the volume production compared to unthinned stands, especially in the first 5-15 years following thinning (Table 3., see also Holmsgaard, 1958; Pretzsch, 2004; Judovalkis, Kairiukstis & Vasiliauskas, 2005; Kairiūkštis & Judovalkis, 2005). Experiments with one single cutting in the young stand with 60-70% basal area removal has been showed to have approximately 10% reduced volume production compared to unthinned control after 20 to 30 years (Eriksson & Karlsson, 1997; Johansson & Karlsson, 2004).

However, results of the studies by Bryndum (1964) (Lindet skov) and Carbonnier & Johansson (1975), indicate that production may be lower if differences in thinning grade is applied later in the rotation, in stands already repeatedly thinned. Bryndum (1964), reports data from an unreplicated thinning experiment started at a mean height of 17 m with light and normal thinning. The volume production in the first 15 years following treatment initiation was similar but with continuous cutting the production decreased considerably in the more heavily thinned plot for the following 17 years. For the whole observation period (32 years) the volume production in the more heavily thinned plot was 92% of the production in the plot with lower thinning grade. The initial ten year volume growth response in a thinning experiment (two blocks) in south west Sweden initiated at a dominant height of 15-20 m was reported by Carbonnier & Johansson (1975). The thinning grades corresponded to extra light, light and heavy (se Table 2 for definition of those thinning grades) and the volume production compared to the light thinning grade was 93% and 73% in light and heavy thinning respectively. Delayed thinnings in very dense stands may also result in slower volume growth recoveries in relation to unthinned counterparts than indicated by the studies listed in table 1-2 (Preuhsler & Schmidt, 1989).

Studies on volume production after thinning in old stands indicates that their productivity will be lower compared to unthinned controls than data from younger stands may indicate (Näslund, 1942; Nilsen & Haveraaen, 1983; Nilsen, 1988). Nilsen & Haveraaen (1983) investigated thinning in stands on three fertile sites in Norway (53-64 years old at breast height) and found that the production decreased by 23-53% over a ten-year period after removal of slightly less than 60% of the standing volume. In older stands on poor soils with low site indices the growth losses amounted to 47% after removal of 58% of the volume (mean values for nine stands). Ten years after selective cutting (removal of the largest trees) with 64% basal area removal (from a basal area level of 23 m^2/ha) in old-mountain-spruce forests the production losses compared to unthinned counterparts amounted to 54% (Nilsen, 1988). It could be argued that heavy selective cutting should allow younger seedlings and small trees to grow and their impact on over storey production could be significant (Elfving, 1990), but still minor compared to the high level of growth loss. It should also be noted that comparing the results of the studies by Näslund (1942), Nilsen & Haveraaen (1983) and Nilsen (1988), with those cited in table 1 is not straightforward since the material they examined was situated on less fertile soils in a harsher climate and with lower basal area at start of the experiment.

Pretzsch (2004) investigated long-term thinning experiments in both Norway spruce and beech stands in Germany. The nine spruce plots were, with one exception, situated close to the Bavarian Alps and had rather high site indices (estimated dominant height at 100 years = 28-36 m). The stands were established with initial square spacings between 0.9 and 1.4 m and the different thinning treatments (A-, B- and C-grade) were initiated at stand ages of 32-43 years. Mean thinning interval was six years. At the last inventory, the oldest stands were over 140 years old. The growth in stem volume is given as merchantable volume (7 cm minimum top diameter). Pretzsch (2004) claims that the growth of Norway spruce follows a unimodal optimum pattern (*c.f.* Langsæter, 1941; Assmann 1970) that is dependent on the site index and ontogenetic stage. A 50% reduction of stand density in young stands may increase the current annual stem volume production by up to 10%, but at the same time the stand is transported "earlier in an advanced allometric stage, so that the potential to react on thinning with transgressive growth subsides prematurely". Thinning with both B- and C-grades resulted in higher current annual growth during the first two decades after treatment initiation. Growth continued to be superior following the B-grade treatment compared to the A-grade treatment over the whole observation period, but the growth rate under C-grade thinning dropped to 95-100% of that under A-grade thinning from 50 years of age onwards. Long-term thinning experiments in Lithuania (Judovalkis, Kairiukstis & Vasiliauskas, 2005) also showed increases in periodical annual volume growth in young stands of all species investigated, including spruce. The data indicate that it is possible to increase production by thinning young (10-20 year old) Norway spruce stands by 30%, but older stands (60-70 years) become more productive if they are left to grow without cuttings. The thinning degree at which the volume growth is maximized is approximately 20% (volume removal) for young stands and <10% for stands between 40-50 years old. This variation may be due to differences in crown architecture and physiological canopy features between old and young spruce stands, since Falge *et al.* (2000), found that transpiration and photosynthetic rates are lower in older trees, due to limitations in the scope for individual tree crowns to expand into spaces with high light availability. The hypothesis that the optimal stand density, expressed by basal area, for growth may increase with increasing age has also been raised and discussed for even-aged plantations of *Eucalyptus marginata* (jarrah) by Stoneman *et al.* (1996).

From the studies cited above, it seems reasonable to conclude that older stands should be thinned less intensively than young stands to avoid production losses. Heavy cutting with 60-70% basal area removal in a single heavy intervention in a young stand should result in small growth losses compared to unthinned stands even in the initial 5-7 years after the treatment (Carbonnier, 1974; Eriksson & Karlsson, 1997; Paper III), but such intense cuttings in older stands will almost certainly result in considerable initial production losses. On the other hand, too early thinnings (before canopy closure), reduce stand growth compared to later thinnings (Braastad & Tveite, 2000, 2001).

Slodicak, Novak & Skovsgaard (2005), reported results from a Norway spruce thinning experiment in the Czech Republic. The experiment was part of the European stem number experiment (Anon, 1977), which differs markedly from most of the studies cited above due to its more practical approach, the aim being to establish thinning experiments close to contemporary management principles including mechanised forestry work. The stand was established at very dense spacing (8775 plants per hectare), but was respaced to 2500 stems per hectare eight years later. The treatments were unthinned control and four different treatments with partially or fully mechanised selective thinning. All treatments were replicated twice. Mechanised thinning in this context does not mean that machinery was used in the stands, but that the thinning regimes were applied in a geometrical pattern that would allow for use of machinery. The first thinning (from below), carried out in 1978 at 10 m top height, removed 40% of the basal area, in three out of four actively thinned plots. In one treatment additional thinning was carried out at 12.5 and 15 m top heights with slightly less than 20% basal area removal in each thinning. Two other plots that were also thinned for the first time at 10 m top height, were thinned a second time at 20 top height and a third time at 22.5 m (13 and 20 years after the first thinning) with 17 and 13% basal area removal in each thinning, respectively. The difference between those two treatments was that 3.5 m wide strip-roads were included in one, and 5 m wide strip-roads in the other. The last treatment was a selective crown thinning that was delayed until an economically viable thinning was possible (extraction of 63 m^3 ha^{-1} with a minimum diameter of 12 cm at breast height). This treatment was followed by a rather intense thinning three years later (removal of 54 m^3 ha^{-1}) and a final thinning two years before the last growth evaluation. The delayed thinning regime resulted in the highest extraction volume, but the lowest total production. The stand volume production in the three treatments thinned in 1978 was similar. Compared to unthinned controls, where total production amounted to 753 m^3 per hectare, the actively thinned plots showed 14-23% losses in production. Less than 5% of total production in the unthinned stand was lost due to natural mortality.

There are interesting reports from other countries in the same experimental series (Eriksson, Johansson & Karlsson, 1994; Skovsgaard, 2006; Dreyfus & Oswald, 2006). In an analyse of all the experiments in the series Herbstritt *et al.* (2006), developed growth equations for the unthinned treatment and the early cuttings with 3.5 m extraction roads. The difference in volume production between unthinned plots and actively thinned plots increased with time and amounted to 10-17% at 25 m top height.

Except for the studiy by Repola, Hökkä & Penttilä (2006), none of the thinning experiments cited above were situated on peatlands (histosols). Therefore, since the reaction to thinning on drained peatlands may differ from responses on upland sites, a thinning experiment on drained peatland was laid out in southern Sweden in 1988. Data from the first 12 years of observation were presented by Landström (2000). Three treatments (unthinned control, 20% basal area removal and 50% basal area removal) were replicated three times. The average stem volume growth per hectare was enhanced by 36% following the light thinning compared to unthinned controls. However, there was no significant difference in stem volume growth per hectare between the heavily thinned and unthinned control stands.

The effects of strip-roads

Use of machinery may lead to soil compaction (Wästerlund, 1992; Landford & Stokes, 1995) and injuries to the fine root system (Ågren, 1968; Wästerlund, 1983, Nadezhdina *et al*., 2006). This may lead to production losses. Kardell (1978) investigated growth losses due to soil compaction and root injuries after use of machinery on a fertile spruce site in south-eastern Sweden. The growth losses during a ten-year period after thinning accounted for 5 to 15 m^3 production reduction depending on the severity of the damage. In some cases, a minor soil disturbance has been reported positive for production (Fries, 1976; Murphy & Firth, 2004) explained with increased rate of nitrogen mineralization (Kardell & Nilsson, 1986). Furthermore, thinning injuries (bark and cambium removal) on stems and coarse roots are reported to cause growth losses (Isomäki & Kallio, 1974; Huse, 1978a; Andersson, 1987).

As well as reductions in volume growth due to disturbance by machinery in the stand *per se*, further losses may occur in mechanised systems because the thinning grade in the road zone is high, the spatial pattern of remaining trees is uneven, site utilization is less efficient than in manually treated stands, and the choice of trees is inevitably sub-optimal in strip-road thinnings (Elfving, 1985; Pettersson, 1996). Most of the long-term thinning experiments cited in table 2, involved selective thinnings in which the removed trees were manually cut and removed out of the plots with minimal use of machinery. Compared to strictly selective thinning, row thinning or cutting of strip roads combined with selective thinning reportedly reduces volume growth (Andersson, 1969; Gallagher, 1976; Bucht, 1981; Spellmann, 1986; Pretzsch, 1995) but for Norway spruce the growth differences between selective thinning and row thinning for a given thinning grade is reported to be small (Niemistö, 1989; Eriksson, Johansson & Karlsson, 1994; Mäkinen, Isomäki & Hongisto, 2006).

Although volume production is maximal if the trees in a stand are regularly distributed (Pretzsch, 1995), line thinning investigations have shown that the spatial distribution in early thinning is relatively unimportant (Elfving, 1985). In pine and spruce stands established in 1.5 m square spacings, Elfving (1985) investigated the effects of a 50% basal area removal in the first thinning either as row thinning with cutting of two adjacent rows or selective thinning. The width of the strip-roads, was 4.5 m. Since the trees to be left in the selective thinning were marked in all plots before decisions were made regarding the treatments, it was possible to separate the effects of reduced selectivity and the effect of unexploited road area on production rate. The selected trees showed 6% higher growth than average trees of the same diameter, and losses in volume growth for row cutting compared to selective cutting amounted to only 4%. The conclusion was that most of the losses in production due to strip roads could be attributed to lower selectivity in the thinning rather than to uneven patterns of remaining trees.

Kramer & Holodynski (1989) investigated the effects of several different systematic and semi-systematic thinnings in a 28-year-old Norway spruce stand on a site of the highest fertility class in Germany, unfortunately unreplicated. The stand was established at 1.5 m square spacing and there were approximately 3,500-4,000 stems per hectare in the stand with a top height of 13 m and basal area of 30 m^2 at the time of first thinning. There were four different treatments: thinning of every 9th and 10th rack combined with selective thinning between the racks, thinning of every 9th and 10th rack in two opposite directions, thinning of every 5th and 6th row and an unthinned control. The first thinning removed 33-35% of the basal area. A selective thinning was conducted five years later, followed by a low thinning after another six years. The mean basal area was approximately the same for all actively thinned treatments and averaged 71% of the basal area in the control plot over the whole 15-year observation period. There were small differences between the strictly geometrical treatments and the combination of strip-road thinning and selective thinning. The volume production over the first five-year period was 10% lower for the actively thinned treatments compared to unthinned controls and 7% lower for the whole 15-year observation period.

Staland & Andersson (2002) investigated a thinning experiment in south-east Sweden, mainly focusing on the total economic outcome from combinations of row and selective cuttings with 10, 15 and 25 m strip road distances (each giving the same total basal area removal), followed by two further thinnings. They found no differences in volume production over a 16-year observation period after the first thinning.

Spellmann & Schmidt (2003) claim that the edge trees after strip-road cutting compensate for most of the loss of productive land area and as long as the thinning is moderate, with only 20-30% lower basal area than unthinned counterparts, the volume production will be only slightly lower, but generate superior assortment structure and higher financial returns.

In the previously cited study by Slodicak, Novak & Skovsgaard (2005), and the German (Baden-Württemberg) version of the same experiment (Herbstritt 2006), reductions in volume production, over 22 and 20 year observation periods, respectively, of 3% were found if the strip-roads used in the first thinning were widened from 3.5 to 5 m. After 17 and 16 years observation periods in the

Swedish and Danish members of the same experiment (Eriksson, Johansson & Karlsson, 1994; Skovsgaard 2006), the corresponding losses were 6% and 9-12% (depending on site index), respectively. Similar production losses, 12%, have also been reported for a similar experiment in Austria (Rössler, 2006) at a total stand age of 46 years.

Given the same thinning intensity, the reported differences between selective and geometrical thinning are rather small. Other factors affecting the timber quality and risks for abiotic and biotic damage may be more important. However, apart from reductions in the height to the first living branch for edge trees and, hence, increases in branch sizes in the lower part of the stem (Eriksson, Johansson & Karlsson, 1994), the quality of the trees closest to strip-roads, as long as they not injured (*c.f.* Fröding, 1992), seems to be similar or even better than that of trees in the interior of the stand, since they tend to be larger, although the stems are slightly less symmetrical (Mäkinen, Isomäki & Hongisto, 2006; Skovsgaard, 2006). Development of asymmetric crowns for edge trees might also be of concern for wood quality (Skovsgaard, 2006).

Many authors have considered the risks for increases in snow and storm damage due to the stand opening with strip-roads (Pettersson, 2003; Gardiner *et al*., 2005). Two growing seasons after thinning in a *Cryptomera Japonica* stand, Satoo, Moroto & Ushiyama (1971) reported a doubled snow damage frequency in row thinning compared to selective thinning. On the other hand, the amount of snow damages, thirteen year after thinning, in an experiment with row and selective thinning in Scots pine, was similar (Bucht & Elfving, 1977). Persson (1975b) reports a slight tendency for increased amount of storm damages in row thinnings with Norway spruce but in the big European stem number experiment in Norway spruce (Herbstritt *et al*., 2006), neither of the different experiments reports any significant increase in either snow- or wind damage frequency if strip roads were widened from 3.5 to 5 m. ‘

Thinning method

As well as thinning intensity, the effects of relative thinning intensity in different diameter classes, the thinning type, on volume production and economic returns have been examined. The thinning quotient is a good descriptor of thinning type, which has been defined in several ways, but all of the definitions describe the relationship between the size of cut stems and remaining stems or the size of stems before cutting. The Swedish National Board of Forestry, SVS, (Anon., 1998) defines the thinning quotient as the quadratic mean diameter of thinned trees divided by the quadratic mean diameter of remaining stems. As discussed earlier, the main thinning method in Sweden and Europe during the last 200 years has been thinning from below. In the comparative thinning studies conducted by most research institutions so-called “crown thinning” was also included. Crown thinning is intermediate between thinning from below and thinning from above (Carbonnier, 1978; Anon., 1998). Even if crown thinning and thinning from above should be regarded as different thinning methods, comparisons between crown thinning and low thinning could to some extent help clarify certain issues relevant to the relative merits of thinning from below and above, especially since the more extreme treatment of thinning from above is quite rare. Theoretically, it could be argued that removal of the largest trees in a stand equates, to some extent, to removal of the best producers. However, not all differences between neighbouring trees in a stand are related to genetic differences. Small differences in site fertility in a stand or random sub-lethal calamities could give rise to initial differences between trees with the same genetic capacity for high growth in the stand. Such initial differences could be amplified by asymmetric competition, leading to substantial differences at the time of thinning (Nilsson, 1993). The selection effect includes both a genetic and an environmental component. Concerns about decreasing growth arising from repeated removal of the largest trees in the stand were raised in the early 20th century (Welander, 1910; Wahlgren, 1914) and intensively discussed in the 1940th (Andrén, 1992). Even later there has been discussion about the risk for growth losses due to negative genetic selection after repeated thinning from above (Jäghagen & Albrektson, 1989). Although thinning from above removes a larger proportion of the genetically superior trees than thinning from below, the removal of large trees has positive growth aspects. It has been shown that a retained cubic metre of trees in a small diameter class has higher stem volume production than a retained cubic metre of a large diameter class (Eide & Langsæter, 1941; Braathe, 1952; Mäkinen & Isomäki, 2004a). The difference between gross primary production and net primary production is higher for older, higher and thicker trees (Cannell, 1989). For tall, mature trees with large diameters, the difference between gross primary production and net primary production is probably larger than for smaller trees, even though their age *per se* has no effect (Eklund, 1952).

In practical experiments the difference in volume production between conventional thinning from below and thinning from above has been found to be small and insignificant. Compared to thinning from below, given the same basal area removal in each cutting, Eriksson & Karlsson (1997) found a slight growth reduction (6%) in Norway spruce stands after repeated thinning from above. Similar results (3% growth reduction following thinning from above) have been reported from a thinning experiment in the southernmost part of Sweden (Kardell, 1998). Based on the oldest thinning experiments in Sweden, Pettersson (1955) concluded that, for Scots pine, thinning from below was superior to thinning from above. In Germany (Schober, 1979, 1980) compared crown thinning and thinning from below in a 60 year-old stand with initial basal area > 55 m^2 ha^{-1} over a 60-year period, and found volume production was 7% lower following the crown thinning. Carbonnier (1954) claims that volume growth reduction is generally 5% lower after crown thinning than after low thinning with the same mean basal area.

A thinning experiment in south east Finland with two replicates of thinning from below and crown thinning, followed for 28 years (started at age 30), showed that thinning form below had 3-10% higher volume growth. However, the proportions of volume removed in thinnings were slightly higher (3-8%) in the plots treated with crown thinning (Vuokila, 1960b).

After an observation period of 22 years, Abetz & Feinauer (1987) compared the results of intensive thinning from above, intensive thinning from below and no thinning in two overcrowded Norway spruce stands with 15.5 and 24.5 m top heights, respectively, at the start of the experiment. In the actively thinned plots cuttings were carried out in 1962, 1971 and 1977. In the stand with the lower top height, the first thinnings from above and below removed 31 and 36% of the basal area, respectively. The second thinning removed all trees in a 2.5 m radius around 400 selected crop trees, resulting in basal area removal of 52 and 29%, respectively. The basal area removals in the third thinning were approximately 25%, and conducted as low thinning in both treatments. Over the whole observation period the growth losses associated with the thinning from above and below, compared to no thinning, were 30% and 12%, respectively. For the stand with a top height of 24.5 m at the start of the experiment the general thinning patterns were similar. The percentage basal area removal was only given for the first thinning and amounted to 32 and 28% in the thinning from above and below, respectively. The mean basal area for the whole observation period compared to unthinned control plots was 69% in plots thinned from above and 84% in plots thinned from below. Compared with the unthinned control plots, the growth was enhanced by 9% after thinning from below but decreased by 16% after thinning from above. However, the cuttings were more intense in thinning from above in the second and third thinnings and one could argue that the differences between the two actively thinned plots was not due to the differences in thinning methods but to the differences in thinning grades (Vuokila, 1970; Eriksson, 1992; Smith, 2003).

In uneven-aged mature stands, crown thinning or thinning from above may even increase growth compared to thinning from below with the same thinning intensity (Näslund, 1942; Lundqvist *et al*., 2007). In a Danish experiment started in an older (77-year-old) previously thinned stand with a rather low site index, thinning from above increased the production over a ten-year investigation period compared to thinning from below even though the cutting intensity was higher in the former (Madsen, 1979). In a Danish investigation by Møller & Holmsgaard (1947) the volume growth after thinning from above, "free thinning" and thinning from below was investigated. No differences in growth rate were found over a 12-year post-thinning period. In experiments in Finland, established in stands previously thinned from below, thinning from above was found to give slightly higher production in pine stands, similar production in spruce stands and lower production in birch stands compared to thinning from below (Vuokila, 1970). Hynynen & Kukkkola (1989) detected no significant differences in basal area growth, volume growth or yield of commercial wood five years after application of thinning from below, above and selection thinning in spruce and pine stands as long as the basal area after thinning was the same in all thinning regimes. In a Norway spruce experiment established in a 46-year-old stand, followed over 21 years, no differences in volume production, production of saw timber or economic returns were found between thinning from below and above with the same periodic mean basal area. The volume increment in pine was enhanced after thinning from above and the growth of birches per unit area was favoured after thinning from below (Mielikäinen & Valkonen, 1991).

Self thinning

To summarize the effects of thinning intensity and method on volume growth per unit area, Norway spruce seems to have a large “biological window”, within which variations seem to have fairly minor effects on production. A further variable that should be taken into account when estimating (or comparing) volume production is the volume of trees that have died due to self-thinning. In most cases, dead wood is unusable and hence the total merchantable yield for different thinning programmes may differ if they result in significantly different volumes of dead trees (Skovsgaard, 1997). Self-thinning occurs due to competition between trees in the stand and it may be argued that estimates of losses due to self-thinning should not include losses due to snow and/or heavy winds (Karlsson, 2005). There is a limit for the amount of biomass that can be accumulated in a stand (Tadaki & Shidei, 1959; Yoda *et al*., 1963; Skovsgaard, 1997; Pretzsch & Biber, 2005) and it has been claimed that the net stand production, in basal area or volume, reaches a peak at intermediate stand densities (Waring, Newman & Bell, 1981). The competition in a stand may be either asymmetric (one-sided) or symmetric (two-sided) (Cannell, Rothery & Ford, 1984; Weiner & Thomas, 1986; Firbank & Watkinson, 1987). Asymmetric competition means that large trees affect smaller ones in larger proportions than indicated from their size alone and this effect is often attributed to competition for light, while symmetric competition emerges when nutrients and/or water, instead of light, is the limiting factor (Nilsson, 1993). According to Shinozaki *et al*., (1964), Valinger (1990) and Nilsson (1993), the allocation to stem growth is relatively higher in suppressed trees than in more dominant trees and after a certain time the retarded crown will be insufficient to provide the tree with the carbon it “requires” so it will die (Boysen Jensen, 1921). Therefore, self-thinning occurs most frequently in unthinned stands and among the smallest trees (Ford, 1975; Kramer & Jünemann, 1985; Valinger, Lundqvist & Brandel, 1994; Eriksson & Karlsson, 1997; Mäkinen & Isomäki, 2004c). Based on data from a previously reported long-term thinning and fertilization experiment in Norway spruce, Eriksson & Karlsson (1997) showed that the early percentage losses from self-thinning in the unthinned stands they examined in southern Sweden increased from 11% at stand ages of 30-35 years to 21% at stand ages of 50 to 55 years. Thirty years after the initiation of a thinning experiment in Norway spruce in south-east Sweden in which 56% of the standing volume was removed in a single intervention the growth losses compared to unthinned controls averaged 30 m^3 ha^{-1} while losses due to self-thinning in the unthinned stand averaged 41 m^3 ha^{-1} (Persson, 1986). It is apparent from above cited studies by Persson (1986) and Eriksson & Karlsson (1997), together with many other thinning investigations (Carbonnier, 1954, 1964; Bergstedt & Jørgensen, 1997; Braastad & Tveite, 2001; Slodičák & Novák, 2003) that regimes with active thinning generate higher merchantable yields than thinning free regimes due to the losses caused by self thinning, snow damages and damages by heavy winds in unthinned stands.

The effects of thinning on wood properties

It is more appropriate to discuss different wood properties, and the effects of thinning on them, rather than quality *per se* (Perstorper *et al*., 1995; Pape, 1999a).

Wood properties are under strong genetic control (Rozenberg & Cahalan, 1997; Hannrup *et al.*, 2004), but growth rates of individual trees and tree properties are highly correlated and since thinning and spacing affect the growth rate of the remaining trees thinning clearly affect tree properties through its effects on growth rates. In addition, thinning also affects tree properties through the selection and removal of trees with undesirable tree properties (Pape, 1999a; Klang, Agestam & Ekö, 2000). The effect of increased thinning intensity on various tree properties, such as knot size, basic density, juvenile wood content, and compression wood in the part of the tree above the base of the crown is similar to the effect of increased initial spacing. There are indications that fast growing trees have larger spiral grain than trees that grow more slowly (Danborg, 1994b). Large spiral grain is considered as a problem when timber is used for construction and therefore thinning from below with high thinning grades will lower the timber quality in this respect (Pape, 1999d; Säll, 2002). For the bottom log, with some exceptions, the increased diameter growth after thinning will in most cases bee positive for the timber quality. Generally, the influence of thinning on tree properties is higher in the regeneration and re-spacing phase (cleaning) of a rotation and near the end of the rotation than during the time of commercial thinning (Klang 2000b). The quality of a stand is also generally maximised by frequent thinnings in each of which small amounts of basal area are removed (Kubler, 1988).

Economic considerations

The main rationale for thinning a stand is based upon the idea that it will increase growth of individual trees and produce more valuable timber and hence improve financial return. The volume and quality production associated with different thinning regimes has a major impact on the overall economic return. However, there is a trade-off between maximal volume production and maximal profitability in forestry (Pettersson, 1962; Riitters, Brodie & Kao, 1982; Cao *et al.* 2006). Thinning involves a trade-off between the best biological results and demands for cost-efficient use of machinery and manpower (Olsson 1986).

There is an almost infinite variety of possible silvicultural programmes. However, the economic superiority of thinned compared to unthinned alternatives, especially with increasing alternative rate of return ("interest rate") has been shown in numerous studies concerning Norway spruce in the Nordic countries in the last 70-80 years (Bornebusch, 1933; Carbonnier, 1954, 1957; Bryndum, 1978; Valsta, 1992; Bergstedt & Jørgensen, 1997; Hyytiäinen & Tahvonen, 2002; Cao et al., 2006), but in Norway, the widely held belief in the positive effect of thinning on economic returns has been questioned (Eid & Eriksson, 1991, Solberg & Haight, 1991; Braastad, 2001).

Eco-physiology and thinning related to climate change and carbon sequestration

Light, water and nutrients

For practical foresters it may be sufficient to know that the stem volume production associated with different thinning programmes is quite similar over a whole rotation period (Table 1.). However, for purely scientific and (probably) practical reasons it is also important to elucidate the physiological factors that influence stem volume production. The key factors include light, nutrients and water, and the key issues to elucidate include the processes whereby trees construct their production apparatus (needles), and the effects of different silvicultural regimes on these processes (Aussenac, 2000). Essentially, resources absorbed by the roots and current needles (with the assistance of the sun) are used to grow more biomass, including more needles and roots. That is a simple statement, but it is important to remember in order to understand the growth responses of individual trees, as well as the stand, after thinning. Since physiological responses for different stimuli are rather similar among tree species and changes in physiology due to thinning in Norway spruce is rather unknown this section will refer to different coniferous and broad-leaved species.

Light

The biomass production of various crops has been shown to be linearly related to the amount of photosynthetic active radiation (PAR) intercepted (Monteith 1977) and this also holds for both stands of trees (Linder 1985, Cannell *et al.*, 1987, Bergh, Linder & Bergström, 2005) and individual trees (Brunner & Nigh, 2000).

The size of the canopy is usually described by the leaf area index or LAI (leaf area per unit ground area, $m^2\ m^{-2}$) and the value of LAI, and its structure, determine the amount- and efficiency of the stand's biomass production (Boysen Jensen, 1921; Waring, 1983; Cannell, 1989; Long & Smith, 1992; McCrady & Jokela 1998). Light interception, and hence production, is non-linearly related to needle mass and LAI, the volume growth in even-aged plantations increases with increasing LAI-value, up to an asymptotic level and than eventually even diminishes with further increase (Linder 1985; Long & Smith 1992; Beets & Whitehead, 1996). Since light interception, and hence production, is non-linearly related to LAI, the initial growth response to thinning depends on whether the cutting is carried out before or after the stand reaches the asymptotic level of LAI (canopy closure). Early thinning, referred to as pre-commercial thinning or cleaning (Fahlvik, 2005), and carried out before canopy closure reduces the growth quite substantially compared to later thinnings (Ruha & Varmola, 1997, Braastad & Tveite, 2000, 2001), but if the thinning is carried out at the asymptotic level of leaf area, the reduction in productivity will be lower than the reduction of LAI.

The needle efficiency, light use efficiency or growth efficiency (ε) describes the amount of above-ground- or stem-volume production per absorbed unit of light, or the ratio of annual photosynthesis to annual intercepted radiation (Waring, Thies & Muscato., 1980; Brix, 1983, Sheriff, 1996; O'Hara *et al.*, 1999). The ε-term has been used to describe thinning reactions (Waring, Newman & Bell., 1981; Lavigne, 1988). The growth of individual trees and the light use efficiency at stand level decreases with increasing LAI (Waring, Newman & Bell, 1981; Binkley & Reid, 1984; Oren *et al.*, 1987; Roberts & Long, 1992; Velazquez-Martinez, Perry & Bell, 1992; Utschig, 2002). In the first growing season after thinning, the lower parts of the crowns of the retained trees will be exposed to a higher amount of PAR than before thinning and thus will partly compensate for the photosynthetic capacity (needle biomass) lost in the thinning (Ginn *et al*., 1991; Lavigne, 1991; Hale, 2001, 2003; Shibuya *et al*., 2005). That is as long as the trees does not experiences thinning stress due to the abrupt changes in light regime for needles adopted to less intense light (Boysen Jensen, 1921; Stålfelt, 1935; Harrington & Reukema, 1983; Aussenac, 2000; Skuodienė, 2001; Lagergren & Lindroth, 2004).

Recovery of LAI after thinning is also most pronounced in the lower part of the crown (Medhurst & Beadle, 2001, Yu *et al*., 2003). Thinning hampers the abscission of the lower branches and since height growth is not strongly affected by the thinning grade the crown length increases more with time in thinned than in unthinned stands (Hummel, 1947; Kramer, 1966; Kantola & Mäkelä, 2004). Trees allocate a higher proportion of their assimilated carbon to canopy development in widely spaced stand (Bernardo *et al*., 1998) and after thinning the remaining trees occupy the created space through expansion of their crowns. According to Judovalkis, Kairiukstis & Vasiliauskas (2005), Norway spruce crowns expand markedly in the second year following thinning, and the rate of expansion declines thereafter, but are still clearly detectable after five years. If the needle efficiency (or light use efficiency) is not changed by the applied thinning regime then the production differences between thinned and unthinned stands will be totally dependent on leaf area and canopy structure. Many authors have found increases in needle efficiency following thinning (van Laar, 1976; Brix, 1983; Velazquez-Martinez, Perry & Bell, 1992; Stoneman *et al*., 1996; Blevins *et al*., 2005) while others have not (O'Hara, 1989; Lavigne, 1991; Waring, Jarvis & Taylor, 1991; Valinger, 1993; Beets & Whitehead, 1996). West & Osler (1995), studying four year post thinning growth response in *Eucalyptus regnans,* found no increase in leaf efficiency on a site that developed a vigorous understorey after thinning while on one site with little understorey there was an effect.

Water

Shortage of soil water reduces the diameter growth of trees (Zahner, 1968; Aronsson, Elowsson & Forsberg, 1978; Alavi, 1999). Throughfall is negatively correlated to stand density and the amount of foliage (Stogsdill *et al*., 1989, 1992; Johnson, 1990; Nadkarni & Sumera, 2004) and varies according to the nature of the precipitation (Calder, 1996; McJannet & Vertessy, 2001). In addition, due to higher amount of leaf area, unthinned stands have higher transpiration rates (Bréda, Granier & Aussenac, 1995; Alavi & Jansson, 1995) and higher interception losses (Alavi & Jansson, 1995) than their unthinned counterparts. Therefore, thinning increases soil moisture in the residual stand. This conclusion is supported by various empirical observations (Brix & Mitchell 1986; Donner & Running 1986; Aussenac & Granier 1988; Cregg, Dougherty & Hennessey, 1988; Bréda, Granier & Aussenac, 1995; Sword, Haywood & Andries, 1998; Thibodeau *et al*., 2000). The increased soil water level in thinned stands reduces water stress for the individual trees (Stoneman *et al*., 1996; Misson, Nicault & Guiot, 2003), although the positive effect of increasing soil moisture on growth at stand level could be questioned in areas with high precipitation. However, as shown by Alavi

(1996, 2002) even areas with high precipitation have occasional water shortages that may have a negative impact on tree growth.

Nutrients

Most forest stands in the temperate region, including Sweden, are nitrogen limited (Tamm, 1991, Gundersen & Bashkin, 1994). However, on fertile sites in the southernmost part of Sweden growth in Norway spruce stands after canopy closure may be limited by K and P rather than N (Persson, Eriksson & Johansson, 1995; Thelin, Znotina & Rosengren, 2000). A high proportion of the total amount of nitrogen in the forest is tightly bound in organic molecules and a limited percentage (<1%) of the total nitrogen pool is available for the trees (Lundmark, 1986).

In long-term thinning experiments in Norway spruce stands evaluated after approximately twenty-five to thirty years, the accumulation of nutrients (N and P) in the forest floor decreased with increased thinning grade according to Wright (1957), and Vesterdal *et al*. (1995), and this conclusion is supported by the results of experiments in the Czech Republic reported by Slodicak, Novak & Skovsgaard (2005). Increased accumulation of nutrients in unthinned compared to thinned stands of Ponderosa and Radiata pine has also been reported (Wollum & Schubert 1975, Carey, Hunter & Andrew, 1982). The decreased total amount of nutrients in the forest floor after thinning could be attributed to higher net mineralization rates (Wright, 1957). It is also possible that reductions in litter fall after thinning affect the nutrient status in the top soil (Novák & Slodičák 2004, Grady & Hart, 2006). However, in stands that are growing well the effect of thinning on litter fall is not long lasting and disappears after canopy closure (Roig *et al*., 2005).

The opening of the canopy after thinning (Johansson 1986) increases the amount of light and thermal radiation reaching the ground (Carbonnier 1933, Fairbairn 1961, Son *et al*., 2004) and consequently increases soil temperatures (Ronge, 1928; Ångström 1937, Sword, Haywood & Andries, 1998). Higher soil temperature and increased soil moisture after thinning provides more favourable conditions for decomposing soil micro-organisms and soil fauna (Bornebusch, 1930; Castin-Buchet & Andre, 1998, Thibodeau *et al*., 2000), which may promote conversion of tightly bound nutrients in the soil into more readily available forms and thus improve soil productivity and increase stand volume growth (Tamm, 1920; Hesselman 1925, Langsæter, 1941; Wang, Simard & Kimmins, 1995; Paul & Clark, 1996; Øyen 2001; Slodicak, Novak & Skovsgaard, 2005).

For various tree species, including Norway spruce, it has been reported that the nitrogen concentration in the needles (or leaves) increases after thinning (Carbonnier, 1954; Velazquez-Martinez, Perry & Bell, 1992; Wang, Simard & Kimmins, 1995; Thibodeau *et al*., 2000; López-Serrano *et al*., 2005). Thirty years after thinning in Norway spruce stands in Belgian Ardennes, the nitrogen concentration in current year needles was significantly decreased compared to unthinned control (Jonard, Misson & Ponette, 2006). Needle nitrogen concentration is related to site fertility (Thelin *et al*., 2000) and increases in the nitrogen content of the needles after thinning increase their net photosynthetic rate and light use efficiency (Wang, Simard & Kimmins, 1995; Beets & Whitehead, 1996; Sands, 1996). The increased production rates of individual trees with increasing nitrogen concentrations in the needles levels off at values of 1.5 to 1.6 % N (Sikström *et al.,* 1998).

The possible additional amount of available nitrogen in thinned stand may not benefit the trees if the cutting is so intense that the forest floor is invaded by plants with a high N-demand (Kardell, 1978; Knoche, 2005). Harvesting residues left after thinning and decomposition of fine roots (Romell, 1938) could change the C/N ratio in the soil and since the mineralization rate is related to both the carbon content and the C/N ratio of the soil (Colin-Belgrand *et al*., 2003), and plants compete for nitrogen with micro-organisms (Kaye & Hart, 1997, Thibodeau *et al*., 2000) the thinning effect on the amount of released inorganic nitrogen over time is complex and may vary for short and long time perspectives. Some studies (cited above) have found indications that nitrogen mineralization increases after thinning, while others have found thinning to have no effects on these variables (Formánek & Vranová 2003) or even inverse effects (Thibodeau *et al*., 2000; Grady & Hart, 2006).

Climate changes and carbon sequestration

Since the middle of the 19th century the use of fossil fuels for energy production has led to sharp increases in CO_2 levels in the atmosphere that will, it is believed, increase global temperatures and change the local climate, including temperature and precipitation patterns (Sonesson, 2004). Such changes may have profound direct consequences for forestry, and indirect consequences due to global, national or local policy responses. In some regions, for instance, stand productivity might increase due to elevated temperature and CO_2, while in other regions stand productivity might be much more strongly limited by water availability than they are now (Zheng *et al*., 2002; Berg *et al*., 2007). Temperatures increases may also increase the risks for injuries due to heavy winds because the ground is less extensively frozen (Nilsson *et al.,* 2004). Spruce is regarded as being particularly sensitive to predicted climate changes (Jacobsen & Thorsen, 2003; Nilsson *et al*. 2004; Kellomäki & Leinonen, 2005; Tatarinov *et al*., 2005; Briceño-Elizondo *et al*., 2006).

In addition, forests may be used in attempts to alleviate the climate changes by increasing the amount of carbon stored in them or using them more intensively for bioenergy production. Forests in boreal and nemo-boreal regions are important sinks for carbon and the amount of carbon stored in them is to some extent dependent on the management regime in several ways (Eriksson, 2006; Hyvönen *et al*., 2007). The soil carbon pool is generally greater than the above-ground component in boreal forest ecosystems, but the accumulation of soil carbon is positively correlated to above-ground biomass production and increases in the above-ground carbon stock are, of course, also preferable in the CO_2 sink context.

In addition, thinning has been shown to reduce the amount of carbon stored in the humus layer (Piene & van Cleve 1978, Carey, Hunter & Andrew, 1982; Vesterdal *et al.*, 1995). However, according to Skovsgaard, Stupak & Vesterdal (2006), the decreasing amount of carbon in the humus layer is counterbalanced by an increasing amount of carbon in the upper (0-30 cm) mineral soil, resulting in no effect of thinning on total soil carbon.

Thinning may be an important tool to meet new climatic challenges in at least two ways. Increasing thinning intensity could increase the soil water content and thus ameliorate the negative effects of increased drought (Lagergren, 2001; Misson, Nicault & Guiot, 2003). In addition, intensive thinning in young stands may also provide scope to reduce the rotation age and hence to switch more rapidly to a different, better-adapted tree species in the coming rotation if necessary. More generally, thinning may also provide greater flexibility, which may be valuable in several respects, not all of which are readily predictable (Jacobsen & Thorsen, 2003).

Risks and calamities in relation to silvicultural regime

Since differences in volume growth for different applied thinning programmes in Norway spruce are minor, and could be regarded as negligible over a rotation period (table 2), other factors are more important for the final economical result. The silvicultural system, especially the thinning regime, affects the risks for injuries by snow and heavy winds (Persson, 1972; Brüchert, Becker & Speck, 2000; Gardiner & Quine, 2000), root rot and other biotic injuries (Vollbrecht, 1994). Taking the risks for butt rot, windthrow, snow damage and/or fire into account will affect the optimal choice of silvicultural regime in terms of financial returns (Thorsen & Helles, 1998; Möykkynen, Miina & Pukkala, 2000; Möykkynen & Miina, 2002; González, Pukkala & Palahí, 2005). Potential financial returns will be overestimated if risks are not taken into account.

Norway spruce is generally considered to be highly susceptible to damages from heavy winds, compared to Scots pine and various broadleaved species for example (Wahlgren, 1914; Jakobsen & Rasmussen, 1953; Prpic, 1969; Peltola *et al.*, 2000; Valinger *et al.*, 2006). However, if the heavy wind strikes at times before the leaves have fallen, the injuries to broadleaved species may be as high as for conifers (Anon., 1969; Nilsson *et al.*, 2004). After a detailed scrutiny of the outcome from the heavy storm that affected Sweden in 1969 combined with an impressive literature review Persson (1975b) concluded that Norway spruce trees are more often felled by wind than Scots pine trees, not (as is often claimed) because of their shallow root systems, but because of the differences in the sites at which the two species are generally dominant.

Risk for damages by snow and heavy winds

Thinning

The risk for snow damage is highest in young stands and the risk for wind damage is highest in older stands (Persson, 1974; Chroust, 1987; Kuboyama & Oka, 2000). Wind damage is a more stochastic phenomenon than damage by snow (Jalkanen & Mattila, 2000). Most authors agree that recently thinned stands, independent of tree species, are in danger for damages from heavy winds (Kollberg, 1961; Leibundgut, 1969; Bradley, 1970; Harrington & Reukema, 1983; Laiho, 1987; Valinger & Lundqvist, 1992; Nielsen & Knudsen, 2004), especially old stands that have been heavily thinned (Sjöström, 1932; Jacobs, 1936; Anon., 1954; Persson, 1975b; Abetz & Unfried, 1984; Chroust, 1987; Nielsen 2001).

Although thinning in young stands with mean heights < 10-12 m gives low wind damage risk (Werner & Årmann, 1955), because of good development of the root system and increased soil anchorage of the remaining trees (Nielsen & Knudsen, 2004), the best way to reduce the risk for heavy wind damage at any given point is probably to leave the stand completely unmanaged without thinnings. Unthinned stands with high degrees of stocking have been shown to resist heavy storms well (Sjöström, 1932; Bornebusch, 1937; Werner & Årmann, 1955; Lohmander & Helles, 1987; Vollbrecht, Gemmel & Elfving, 1994; Bergstedt & Jørgensen, 1997; Skovsgaard, 2006). However, to obtain the desired value from the forests without thinnings, it is important to establish the stands with wide initial spacing or to apply early pre-commercial thinning to improve stand stability (Anon., 1969; MacKenzie, 1976; Skovsgaard, 1997; Nielsen, 2001; Achim, Ruel & Gardiner, 2005). The no-thinning option has been adopted in stands at high risk for damage by wind and snow, or where it is not possible to obtain a profit from early selective thinnings (Skovsgaard, 1997; Cameron, 2002). Since it is well known that the increased risk for injuries due to heavy winds directly after thinning decreases again with time (Bradley, 1970; Persson, 1975b; MacKenzie, 1976; Nielsen & Knudsen, 2004), some authors have claimed that it is possible to increase stands' resistance to storms by early, heavy thinnings (Hütte, 1970; Bergstedt & Jørgensen, 1997; Nielsen *et al*., 2004). Nielsen & Knudsen (2004) investigated a Norway spruce stand thinned at approximately 16 m height with a 75% reduction of stems and found that the remaining individual trees doubled their stability in the first five years after cutting, but the increased risks for storm felling at stand level due to reductions in support from neighbouring trees and increased wind speeds exceeded this effect. Thus, as is often the case, silvicultural measures that could influence the stability of individual trees and stands generally have conflicting effects (Nielsen *et al*., 2004).

Reductions in stand density, either by increased initial spacing or thinning, affects diameter growth more than height growth (Lanner, 1985; Huss, 1988; Slodicak & Novak, 2006) and thus lead to reductions in the trees' height to diameter (H/D) ratios (Tuyll & Kramer, 1981; Spellmann & Brokate, 1991; Mitchell, 2000; Slodicak & Novak, 2006; Mäkinen & Hein, 2006). A low H/D ratio is often used as an indicator of good tree stability (Kramer, 1976; Cremer *et al*., 1982; Spellmann, 1986; Valinger & Fridman, 1997; Nielsen, 2001; Slodičák & Novák, 2004; Valinger *et al*., 2006). Prpić (1969) found that windthrow in Norway spruce was related to slenderness, tree form and relative crown length. The lower the values of those parameters, the greater the tree stability. It has been claimed that H/D ratios < 80 should be targeted to minimize the risk for damages due to heavy winds (Prpić, 1969; Burschel & Huss, 1987; Abetz & Klädtke, 2002) and snow (Päätalo, Peltola & Kellomäki, 1999). Schütz *et al*. (2006), report that in heavy storms (average maximal wind speed > 45 m s^{-1}) reductions in H/D ratios and the time since the last thinning did not have any significant effects on the risks for windthrow and stem breakage. The same was found for a thinning experiment in Norway spruce in Denmark and Skovsgaard (2006), claim that "the analysis of h/d-ratios and similar stability indicators is of little practical relevance.

Dense stands with high degrees of stocking have high risks of snow damages (Hesselman, 1912; Schotte, 1916; Spellmann, 1986; Valinger, Lundqvist & Brandel, 1994; Slodičák & Novák, 2004; Rössler, 2006) and even though newly thinned stands are at risk for snow damages (Schotte 1916, 1922b; Chroust, 1987) increased spacing in young stands and repeated thinnings over a long time gives the trees well-developed crowns and low H/D ratios, which decrease the risk for snow damages (Schotte, 1916; Chroust, 1987; Päätalo, Peltola & Kellomäki, 1999; Braastad & Tveite, 2000; Kato & Nakatani, 2000). Except in the first few years, thinning from below decreases the risk for snow damages (Hesselman, 1912; Persson, 1972; Bryndum, 1976; Spellmann, 1986; Huss, 1990; Zhang & Oliver, 2006), while thinning from above or crown thinning is reported to increase the risk (Schotte, 1916; Amilon, 1926; Persson, 1972; Valinger, Lundqvist & Brandel, 1994). Thinning from above also increases the risk for storm damages since the removed trees are those best adapted to resist heavy winds (Welander, 1940; Persson, 1972; Madsen, 1979; Nielsen *et al*., 2004).

Initial spacing

According to Gardiner & Quine (2000) the differences in injury levels after different thinning regimes is more important than differences due to initial spacing. However, Nielsen (2001) claims that reductions in initial spacing decrease the root development in a way that affects the stability over the whole rotation.

As argued previously, lowering the H/D ratio either by increasing initial spacing or early cuttings has been tested as a potential way to improve stand stability (Bornebusch, 1933; Vollbrecht, Gemmel & Elfving, 1994; Nielsen *et al*., 2004). Heavy thinnings to relative basal areas between 35-45% of unthinned counterparts, commencing early in the rotation period leaving an intact green crown have been shown to decrease damages due to heavy winds (Bergstedt & Jørgensen, 1997; Nielsen, 2001).

Fewer planted trees per hectare imply fewer thinnings and a shorter rotation period, which help reduce risks for storm injuries (Lohmander & Helles, 1987). Moreover, the increased planting distance *per se*, regardless of the thinning regime applied, will lower the risk for injuries due to heavy winds (Blackburn & Petty, 1988; MacCurrach, 1991; Gardiner & Quine, 2000) and snow (Braastad, 1979; Kramer, 1980).

Risk for infection by root- and butt rot

Thinning

One of the major threats to Norway spruce plantations in southern Sweden is root- and butt rot (mainly *Heterobasidion* spp.). Around 15% of mature Norway spruces in Sweden are reported to be infected by this fungus (Euler & Johansson, 1983; Stenlid & Wästerlund, 1986). Infected trees are less valuable both as sawn timber and pulp wood (Björkman *et al*., 1949), and further losses will occur due to decreased growth (Henriksen & Jörgensen, 1953; Bendz-Hellgren & Stenlid, 1995, 1997). Root rot was not a major concern of the studies underlying this thesis but a thesis entitled "thinning of Norway spruce" must at least briefly discuss the connections between root rot and thinning since thinning is considered the major infection route for *Heterobasidion* spp (Korhonen *et al*., 1998; Berglund, 2005).

The connection between thinning grade and incidence of root rot is well known (Bornebusch, 1937; Henriksen & Jörgensen, 1953; Molin, 1957; Bryndum, 1964; Venn & Solheim, 1994). Heavier and repeated cuttings have been shown to increase the amount of butt rot in the final stand (Vollbrecht & Agestam, 1995, Vollbrecht & Jørgensen, 1995). So far, however, I have not seen any studies or discussions about whether it is preferable to apply a single heavy cutting or two less heavy cuttings giving the same mean periodic basal area over time, in order to minimise the level of root rot. Some Danish experiments (Bryndum, 1964, 1969) indicate that root rot is heaviest following D-grade cutting, and its incidence is lower following so-called L-grade thinning ("wind break cutting"). We know that heavier and repeated cuttings increase the risk for windthrow, a single heavy cutting in early development stages is better, in terms of the overall risk level than repeated, but less intense, cuttings over the whole rotation (Nielsen, 1990). An interesting issue is whether or not this also applies to the risk for heavy attacks by root rot. Fresh stumps are highly susceptible to root rot infections, which often spread to the dead or dying root system (Rishbeth, 1949; Brandtberg, Johansson Seeger, 1996; Berglund & Rönnberg, 2004) and may subsequently spread further, via root contacts, to standing trees (Rishbeth, 1951; Molin, 1957). The most important route for root rot infection in an even-aged plantation is believed to be either the above mentioned pathway or via infected roots and stumps in the previous stand to the newly established generation of trees (Rönnberg & Jørgensen, 2000).

Superficial injuries to stem and roots caused by logging machines or game may also provide entry points for *Heterobasidion* spp., as long as the wounds are fresh (Hagner, 1965; Nilsson & Hyppel, 1968; Isomäki & Kallio, 1974; Roll-Hansen & Roll-Hansen, 1980a). That pathway is however reported to be quite insignificant in comparison to other possible infection routes (Redfern & Stenlid, 1998). Other rot fungi could also be important contributors to the overall rot infection rate if the stand is heavily damaged by game or logging machines (Kohnle & Kändler, 2007). Thinning injuries to stems and roots and associated problems with discoloration and/or decay will be addressed later in this thesis. Root- and butt rot increases the risk of storm damages (Jakobsen & Rasmussen, 1953; Bryndum, 1964; Bazzigher & Schmid, 1969; Vollbrecht, Elfving & Gemmel, 1994, Cermák, Jankovský & Glogar, 2004).

Initial spacing

Wider initial spacing when replanting previously root rot-infected forest land has been found to reduce the frequency of butt rot in the maturing stand (Due, 1960; Høibø, 1991b; Venn & Solheim, 1994; Johansson & Pettersson, 1996). However, in the cited studies there were interactions between the effects of initial spacing and thinning regimes (a more frequent thinning schedule is needed in denser stands). A possible explanation of the lower butt rot frequency in plantations with wide initial spacing is that there are likely to be fewer root contacts between infected and uninfected trees (Korhonen *et al*, 1998). Therefore, even experiments with mixed stands could help elucidate whether a wider initial spacing *per se* could reduce butt rot frequency. Studies in mixed stands with spruce and pine (Lindén & Vollbrecht, 2002) have found lower butt rot frequencies in the spruces than in monocultures, which may, hypothetically, be due to the longer distance between the spruces, the species with the highest risks for infection.

Injuries to stem and roots from logging machines

The positive aspects of thinning may be jeopardized if the thinning is not done with sufficient knowledge and care. Previously mentioned risks for introducing root rot to a stand and the enhanced risk for storm felling are important aspects to consider. Further usually directly detectable, negative effects on the stand of thinning may include site damage and soil disturbance due to forestry traffic (Kardell, 1978; Wästerlund, 1992; Wilpert & Schäffer, 2006; Nadezhdina *et al*., 2006) and injuries to stem and roots in the remaining trees (Andersson, 1980; Fröding, 1992; Vasiliauskas, 2001). Although thinning, regardless of how it is done, may damage the residual stand, it was the increased mechanisation of forestry after the Second World War that, in Sweden at least, prompted investigations of injuries to the stems and roots of the remaining trees after partly mechanised thinning (Bengtsson, 1955; Carlsson, 1959). The structural transformation of society in the 1970s also affected the forestry sector; rising salaries accelerated mechanisation and the development of new systems for clear cutting and thinning. Increased use of machinery in the stands combined with a forestry law stipulating that the frequency of injured trees should not exceed 5% led to a need for more detailed information about injury levels in thinned stands. The injury levels associated with the use of different machines and thinning systems were investigated in a number of studies in Sweden (Kardell, Drakenberg & Dehlén, 1977; Boström, 1978; Arvidsson & Spahr, 1980; Eriksson, 1981; Fröding, 1982, 1983, 1992), Norway (Sellæg, 1974; Huse, 1978b) and Finland (Kärkkäinen, 1969a, 1969b; Hannelius & Lillandt, 1970; Sirén, 1981, 1982, 1986, Imponen & Sirén, 1983) and attempts were made to find correlations between injury frequencies and site types, machinery systems, tree species, cutting seasons etc.

Of all machinery systems used in forestry twenty years ago, the cut-to-length system using harvester and forwarder was to become the most widely utilised in Sweden by the late 1980s (Anon., 1991, Nordlund, 1996) and it has continued to dominate. The majority of studies on cut-to-length systems using harvesters and forwarders in the Nordic countries have reported injury frequencies of around or below 5% (Table 1, paper IV).

Compared to reported injury levels associated with the cut-to-length system with harvester and forwarder in the United States (usually 25-46%) (Bettinger & Kellog, 1993; Youngblood, 2000; Camp, 2002; Heitzman & Grell, 2002), the reported injury levels after thinning in the Nordic countries are low. However, similar results to those reported in the Nordic countries can also been found in the literature from the United Sates (McNeel & Ballard, 1992; Landford & Stokes, 1995). High injury rates for other types of thinning systems have also been reported (Kelly, 1983; Ostrofsky, Seymour & Lemin 1986; Cline *et al.*, 1991; Nichols, Lemin & Ostrofsky, 1994; Bragg, Ostrofsky & Hoffman, 1994; Egan, 1999; Matzka, 2003) and the cut-to-length system using harvester and forwarder is considered advantageous since it generally gives better silvicultural results and similar productivity, but disadvantageous due to the high initial investments required (Tufts & Binker, 1993; Landford & Stokes, 1995, 1996). A study of thinning with a cut-to-length system using harvester and forwarder in five pine stands in Poland found an injury level of 7.8% (Gapšyte, 2003). In permanent Norway spruce experimental plots in Germany (Baden-Württemberg), the total injury level caused by yarding and felling was 27%, and the accumulated percentage of injuries in 61-80 year-old Norway spruce stands obtained from data in the Federal forest inventory (Baden-Württemberg) was 30% (Kohnle & Kändler, 2007). All systems for mechanised thinning seem to injure the remaining trees, but cut-to-length systems with harvester and forwarder are generally considered to have relatively low negative effects on the stand.

Negative impact of thinning injuries

Even though the dominant rot fungi invading Norway spruce are *Heterobasidion* spp. (Kallio & Norokorpi, 1972; Kallio & Tamminen, 1974; Stenlid & Wästerlund 1986), which seldom invade stem and root injuries (Redfern & Stenlid, 1998), a high incidence of stem and root damages are followed by invasion of other rot fungi, *e.g. Stereum sanguinolentum* (Alb. et Schw.: Fr.). Kohnle & Kändler (2007), found that 93% of Norway spruce trees with injuries from felling or yarding were infected by rot at the basal cross-section while 51% of uninjured trees were affected. *Stereum sanguinolentum* (Alb. et Schw.: Fr.) is the most common fungus infecting artificially created wounds (blazing wounds) (Ekbom, 1928; Roll-Hansen & Roll-Hansen, 1980a, 1980b, 1981; Solheim and Selås, 1986; Solheim, 1987), thinning wounds (Huse, 1978a; Ali El Atta & Hayes, 1987; Koch & Thongjiem, 1989; Vasiliauskas, 1998) and bark peeling wounds caused by game (Vasiliauskas, Stenlid & Johansson, 1996; Vasiliauskas, 1998; Čermák, Glogar & Jankovský, 2004). The fungi micro-flora in wounds is reviewed by Huse (1978a) and Roll-Hansen & Roll-Hansen, 1980a, 1980b).

The risk for infection and spread of discoloration increases with the size of the injury (*e.g.* Pawsey & Gladman, 1965; Isomäki & Kallio, 1974; Vasiliauskas, Stenlid & Johansson, 1996). If the damage extends into the wood fibres the risk for infection and spread of discoloration is further enhanced (*e.g.* Pawsey &

Gladman, 1965; Meng, 1978; Roll-Hansen & Roll-Hansen, 1980b). For roots, the risk of fungal infection increases when the point of damage is close to the stem (Hagner *et al*., 1965; Nilsson & Hyppel, 1968; Schönhar, 1979; Koch & Thongjiem, 1989) and the spread of decay is higher in large roots (Hagner *et al*., 1965). The risk for rot infection varies between locations (Roll-Hansen & Roll-Hansen, 1981; Solheim & Selås, 1986; Hennon & DeMars, 1997) and the time of the year when the injury occurs (Roll-Hansen & Roll-Hansen, 1980a, 1980b; Solheim & Selås, 1986; Solheim, 1987; Vasiliauskas, Stenlid & Johansson, 1996). It is also affected by the presence of other fungi or bacteria that may protect the tree from more severe rot fungi and the effectiveness of the tree's own defences (Kallio, 1974; Hennon & DeMars, 1997; Vasiliauskas & Stenlid, 1998).

Huse (1978a) showed that injuries larger than 50 cm^2 are often infected by rot fungi, while smaller injuries are infected less frequently. However, discoloration of the wood due to bacteria or other fungi was detected in all injuries. Nilsson and Hyppel (1968) investigated ten-year-old injuries in the lower part of the stem and the coarse roots after mechanised soil scarification. Major rot attack was present in 100% of the injuries in the lower parts of the stem, regardless of whether they were superficial or deep enough to reach the fibres (however, only four injuries were investigated). Root injuries 0-50 cm from the stem were severely infected by rot in all cases when injuries were deep, but only 13% of the superficial injuries in roots led to major rot infection. In addition, 30% of the scars were infected by rot to a limited extent. For injuries between 50-100 cm from the stem the risks for infection were low; less than 20% of the deep injuries at that distance led to major rot infection. It has been claimed that injuries smaller than 10 cm^2 do not become infected by rot fungus (Meng, 1978). However, Roll-Hansen and Roll-Hansen (1980a) found that up to 15% of 10 cm^2 large stem injuries were infected by *Stereum sanguinolentum* (Alb. et Schw.: Fr.) When infections with other rot fungi were included, the total infection rate in this small class of injuries was almost doubled. In another study by Roll-Hansen & Roll-Hansen (1981) 15% of root injuries with sizes between 4-90 cm^2 became infected by *Stereum sanguinolentum* (Alb. et Schw.: Fr.) and there were no significant size-related variation in frequencies within this range. Pawsey and Gladman (1965) studied injuries to stem and roots ranging in size from 6.5 cm^2 to over 2000 cm^2, and found an infection rate by important rot fungus slightly higher than 9 % for Norway spruce. Although bigger injuries had a higher amount of infected scars, there was no minimum size for injuries with rot fungus. Leinss (1991) found infection rates as high as 22% in injuries smaller than 10 cm^2. Solheim and Selås (1986) studied artificially created stem injuries between 80-400 cm^2 in size and found, two years after the injury events, that almost 60% of the trees were infected by at least one rot fungus. According to a literature review by Vasiliauskas (2001), 60-100 % of wounds inflicted on trees will lead to staining and/or decay.

The annual growth rate of *Stereum sanguinolentum* (Alb. et Schw.: Fr.) in stems of Norway spruce is reported to be between 5 and 75 cm per year with an approximate mean value of 30 cm per year (see Vasiliauskas, 2001 for literature review). Similarly to the risk of infection, the growth rate of the fungus is also dependent on the size and severity of the damage (Hagner *et al*., 1965; Ali El Atta

& Hayes, 1987). The rate of decay is less pronounced in roots (Kärkkäinen 1971) and not all root injuries infected with rot fungi will reach the trunk (Björkhem *et al*., 1974; Roll-Hansen & Roll-Hansen, 1981; Kardell, 1986). Even if small injuries become infected by rot fungi (Pawsey and Gladman, 1965; Roll-Hansen & Roll-Hansen, 1980a; Koch & Thongjiem, 1989; Leinss, 1991), the extent of decay may be limited since the wound closure rate is high for small injuries (Aufsess, 1978; Neely, 1979) and further fungal development after wound closure is limited (Löffler, 1975; Roll-Hansen & Roll-Hansen, 1980b). Stem injuries smaller than 15 cm^2 will have some effect on tree quality, but root injuries of this size will probably have very little effect.

The economic losses due to poor quality and the amount of wood that becomes unusable because of rot following thinning wounds depend on how many bottom logs are destined for pulpwood rather than timber production. Such losses may also include production losses (Isomäki & Kallio, 1974; Huse, 1978a; Andersson, 1987). However, the trees that would have become infected by root rot from nearby stumps or trees regardless of stem and/or root injuries should not be included when summing injury-related losses. Furthermore, root injuries will only cause quality losses if subsequent infection by a rot fungus spreads to the stem. However, stem injuries will reduce the quality of the log even without infection by severe rot fungus (Blomqvist, 1984; Shigo, 1984; Warkotsch, 1988; Han et al., 2000; Vasiliauskas, 2001), although if an injury is situated at either end of the log it is possible to reduce the length of the log without reducing its grading. Earlier studies with harvester/forwarder systems have shown that most stem injuries are located near the ground (Fröding, 1992; Bettinger & Kellog, 1993; Sawaguchi, Shishiuchi & Kikuchi, 2000; Heitzman & Grell, 2002; Suadicani & Nordfjell, 2003). However, such length reduction is only possible if decay has not spread from the injuries, and thus the actual number of possible length reductions will be lower than the frequency of injuries near the ground may suggest.

Objectives

The objective of this thesis was to investigate volume and quality outcome from different thinning strategies in monocultures with Norway spruce. Questions investigated were:

1. How will the combined effect of initial spacing and thinning regime affect timber quality?

2. How is the initial growth response, after different thinning grades, both at tree and stand level, related to light, water and nutrients?

3. How is long term production affected by different thinning programmes?

4. How are risks for biotic and abiotic damages related to different thinning programmes?

Summary of the papers

Paper 1

Numerous studies have explored the relationships between initial planting density, growth and wood quality. For Swedish conditions, these variables have been thoroughly studied in stands with spacings between 1- and 2.5 m, but few investigations have been extended to initial square spacings of 3 m. It is well known that differences in volume production between different initial spacings emerge, to a large extent, in the first part of the rotation period (up to the time of canopy closure) and thereafter the relative differences between total production in dense and sparse spacings diminishes. Similar trends have been observed in comparisons of quality traits. However, since many of the most important quality traits are strongly correlated to the growth rate of individual trees, and to a lower extent to the spacing itself, comparisons of the mean quality in stands with different spacings may be misleading. Different initial spacings occasion different thinning programmes and it is important to consider all silvicultural measures over a rotation period in attempts to identify systems that provide acceptable volume production, quality parameters and low reforestation costs. In addition, the selection methods used in thinning operations will also affect the cost-effectiveness of cutting activities and influence the quality of the remaining stand.

The objective of the study reported in Paper I was to examine the combined effects of the initial planting density and the thinning method used in the first thinning on volume production and quality. More specifically, a conventional silvicultural regime, giving 1800-2400 stems at the time of first thinning (mainly from below) was compared with a regime involving sparse spacing, 1400 stems per hectare, and thinning from above, to assess whether the latter silvicultural regime could provide acceptable quality in the remaining stand.

Material and methods

The experiment was conducted in two fertile stands (G 32) at Tönnersjöheden experimental forest in south-western Sweden (latitude 56º 40'N, longitude 13º 10'E). The stands were planted in 1971 with 2.0, 2.5 and 3.0 m square spacings. Each stand was divided into two blocks. Before thinning in winter 2004, 6, 8 and 12 plots with 10 m radii were laid out in 2.0, 2.5 and 3.0 m initial spacings, respectively. Four additional plots were laid out in the 3 m spacing since we hypothesised that volume production and quality would be least homogeneous in the stands with the sparsest spacing. One block with 2 m spacing had been thinned earlier and had to be excluded from the study. For the 2 and 2.5 m spacings, both thinning from below and thinning from above were applied, whereas in the 3 m spacing, thinning from above and a no-thinning regime were used. The aim was to remove the same percentage of basal area in each treatment (approximately 30%). However, the thinning removed a significantly higher percentage of basal area in the 3 m spacing compared to the 2.5 and 2 m spacings (40, 32 and 28%, respectively).

On every plot, all trees were callipered at breast height and height was measured on sample trees. The height and height to the first living branch of sample trees was measured. The diameter of the largest branch in one of the three whorls closest to breast height was measured as well as the number of branches with diameters ≥10 mm in those whorls. The frequencies of stem defects such as double stems, spike knots and stem cracks were registered. Additional data were collected from a total of 104 cut sample trees covering the diameter distribution in all three spacings. Each sample tree was cut into two logs, each approximately 4 m long, and graded according to the Swedish grading system by a professional grader. The grading system divides logs of Norway spruce into four classes where quality 1 is the best quality and quality 2 refers to logs with living branches (not bottom logs). Since quality class 1 (highest quality) is rare the main boundary of interest in the present study was the one between classes 3 and 4. It seems reasonable to assume that logs graded in quality 3 and 4 will largely remain in their given quality class until final felling while the quality of logs graded in quality 2 (second log) with living branches will change as the height to the first living branch increases. After grading, a stem disc was taken at 1.3 m stem height and year rings were measured. A crookedness index, calculated as bow height divided by log length, was calculated for each log. The height of the callipered trees was predicted using Näslunds height curve (Näslund 1936) that was fitted for the cut sample trees. Thereafter, stem volume for each tree was calculated with Brandels volume function (Brandel 1990) using measured diameter and estimated height.

Results

Increased spacing resulted in trees with larger breast height diameters and larger knots. The average diameter of the thickest branch in the 2 and 2.5 m spacings was similar (15.7-16.2 mm), but it was significantly higher in the 3m spacing (19.6 mm). The diameter of the thickest branch for trees with the same DBH was increased in the 3 m spacing but the effect of spacing *per se* was rather small. The number of branches was slightly, but insignificantly, affected by initial spacing. From the sampled stem discs it was clear that the main growth differences between the treatments were declining. Increased spacing increased the crookedness index, but the crookedness was strongly related to DBH. The grading of the logs was also clearly dependent on the trees' diameter at breast height, for instance all the trees graded as quality 4 were relatively large. The volume production up to the time of first thinning was 236, 206 and 222 m^3 per hectare in the 2.0, 2.5 and 3.0 m initial spacings, respectively; these differences were not statistically significant. Thinning from above significantly affected the mean DBH in all three treatments and hence the wood quality. Neither the mean diameter at breast height nor the average diameter of the thickest branch was significantly different after thinning from below in the 2 and 2.5 m spacings, and the 3 m spacing after thinning from above. The percentage of logs graded as quality 3 was still higher after thinning in the denser spacings with thinning from below compared to the 3 m spacing with thinning from above, but the differences had diminished.

Papers II and III

The long-term growth responses of Norway spruce stands to thinning is well known but the initial growth responses and the reasons for them are seldom investigated and discussed. The aim of the studies described in Papers II and III was to examine the initial growth responses of Norway spruce to thinning in relation to needle mass, light, nutrients and water. A heavy storm ("Gudrun") on the night between the 8th and 9th of January 2005 destroyed the original experimental plan, but also provided opportunities to investigate the growth and resource allocation in more detail.

Material and methods

The experimental stand (2.5 ha) was located at the Tönnersjöheden experimental forest in south-western Sweden (latitude 56º 40'N, longitude 13º 10'E) and was planted in June 1973 with 4-year-old bare-root seedlings at regular 2.0 x 2.0 m spacing. Before thinning in February 2002, the stand density was 2260 trees ha^{-1}, the basal area was 33.6m^{2}ha^{-1} and the dominant height was 16.4 m, with little variation between the plots. Norway spruce accounted for more than 99% of the basal area before thinning. The thinning from below was done using harvester and forwarder. Three growing seasons were included in the study. The experiment was replicated four times with three treatments (in total twelve 22 x 20 m plots, each containing 11 rows of trees. The treatments were unthinned, normal thinning (30% basal area removal), and heavy thinning (60% basal area removal). In each thinned plot all trees in the middle row were cut, the area thus cleared was used as a strip-road and selective thinning was carried out between the roads. All harvesting residues were placed in the roads. (See Figure 1 for a map of the stand and the plots).

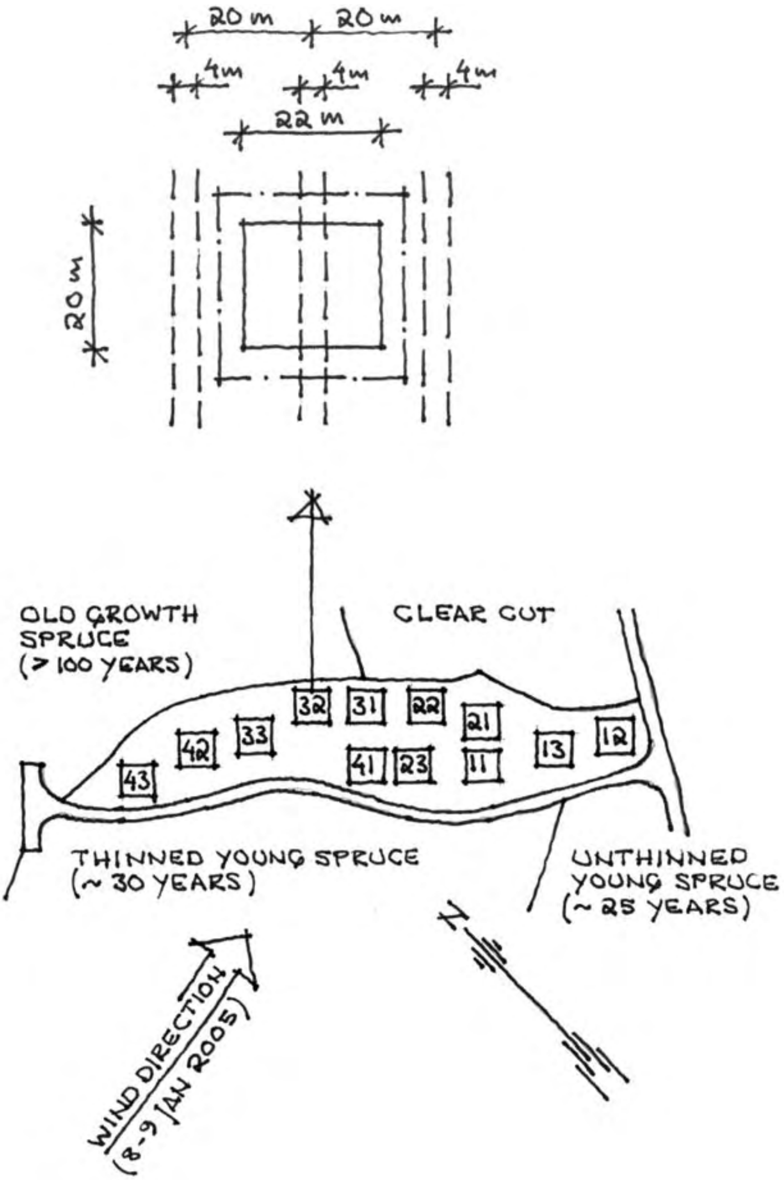

Figure 1. Description of experimental design. The first number in the plots refers to block 1 to 4 and the second number refers to the treatment (1 = control, 2 = normal and 3 = heavy

All trees were numbered and callipered at breast height before thinning and after each growing season. Band-dendrometers were installed on trees covering the diameter range for each treatment to measure growth during each year (weekly during the growing season). Before initiation of growth in 2002, 12 trees were felled for biomass analyses. After the heavy storm in 2005, a total of 53 trees covering the diameter range for each treatment were taken for biomass calculations and estimations of volume growth. The litter fall was collected and included in the total above-ground production calculations. In addition to estimates of needle mass, LAI and light transmission were measured (data were presented for both the first and third growing seasons). The soil water content integrated over the first 50 cm of the soil profile was measured weekly during the growing season. Soil temperature and the amount of inorganic nitrogen released in the top soil were also measured. Temperature data were given only for the first and third growing seasons. Data on inorganic nitrogen (NH_4^+ and NO_3^-) contents and mineralization were collected three times each year at two-month intervals, starting in spring. The nitrogen content in the needles three years after thinning was analysed.

Results

Both normal and heavy thinning resulted in significant initial volume growth retardations. In the first growing season following heavy and normal thinning the volume growth amounted to 47 and 68% respectively of the growth in the unthinned control treatment. The volume production in the second growing season was still lower in thinned plots, but less markedly, and the differences in this respect between normally thinned and control plots were not significant. In the third growing season the growth was not significantly different between normally and heavily thinned plots, but it was significantly higher in normally thinned than in unthinned plots. Mean growth values in the normally and heavily thinned plots over the whole post-thinning period amounted to 90 and 74% of unthinned control levels, respectively. There was no growth reduction related to the cutting of strip roads following either normal or heavy thinning. On the contrary, in the heavily thinned plots, volume growth per hectare in the parts of the plots including the road and one tree row on either side was twice as high as in the three innermost rows. This may have been, partial at least, because the harvesting residues in strip roads led to increased release of inorganic nitrogen, and the soil water contents were slightly higher in the strip-roads in both the normally and heavily thinned plots than in the controls. The soil water contents were similar in unthinned and normally thinned plots (excluding the roads) but they were higher in the heavily thinned plots, especially in dry periods.

The trees in the heavily thinned stands allocated a higher proportion of their stem growth to their most basal parts, thereby increasing the taper between breast height and the stem base. However, there were no thinning-related changes in stem form in the middle stem section, but a slight reduction in taper above the crown base. The overall stem form of the trees was not significantly altered by thinning. The total above-ground biomass production of branches increased following thinning. The amount of new needles produced during the study period was higher in unthinned than in thinned plots, but the canopy needle mass in the heavily thinned plots shifted towards that of their unthinned counterparts due to increased longevity of the needles. After thinning in 2002, the needle mass in the canopy layer was reduced by 25 and 59% in the normally and heavily thinned plots compared to the unthinned controls. After three growing seasons the needle mass in the normally and heavily thinned plots amounted to 77 and 71%, respectively, compared to the unthinned controls. The amount of new needles produced in the control plots equalled the needle losses. The nitrogen content in the needles increased with increasing thinning grade.

In the third growing season, the stand growth efficiency (volume or above ground biomass production per unit needle mass or unit of absorbed light) calculated on the basis of needle mass, LAI or light transmittance, was higher in the heavily thinned than in the normally thinned and unthinned control plots.

The relative basal area growth was affected by both the treatments and the initial basal area of the individual trees. In the control and normally thinned plots, the relative basal area growth of the largest trees was greater than that of the smaller ones. Trees in the heavily thinned plots had similar growth rates regardless of their initial size. The mean growth response of the 100-400 largest trees over three growing seasons in the normally thinned plots was the same as in the control, but growth was significantly higher in the heavily thinned plots.

Storm and snow damage (Papers I, II and III)

The trees in both the combined spacing and thinning experiment (Paper I), and the thinning experiment with different thinning intensities (Papers II and III) described in this thesis sustained injuries due to the heavy storm on the night between the 8 and 9th January of 2005. Further injuries due to wet snow, in March 2005, were recorded in the latter experiment. There was one growing season between the thinning and storm felling in the spacing experiment and three in the thinning intensity experiment. According to Anon. (2005) the maximal wind speeds as a mean value for 2-3 seconds at 10 m height above ground was 32.5-35 m s^{-1} during the storm.

The injuries were categorised as follows: uninjured, leaning, heavy leaning, up-rooting and stem breakage. The difference between leaning and heavy leaning was subjectively determined, depending on whether the tree concerned was believed to be cut in the cuttings following the storm or not. In the final evaluation, injured trees were defined as trees that were heavily leaning, up-rooted or had broken stems.

In the thinning experiment (Papers II and III) there was a strong linear relationship between thinning intensity and storm injuries. The frequencies of snow injuries in March (calculated as percentages of remaining trees) were also strongly correlated with the thinning intensity (data not shown) and hence the total damage percentage remained linearly correlated with thinning intensity (Fig. 2).

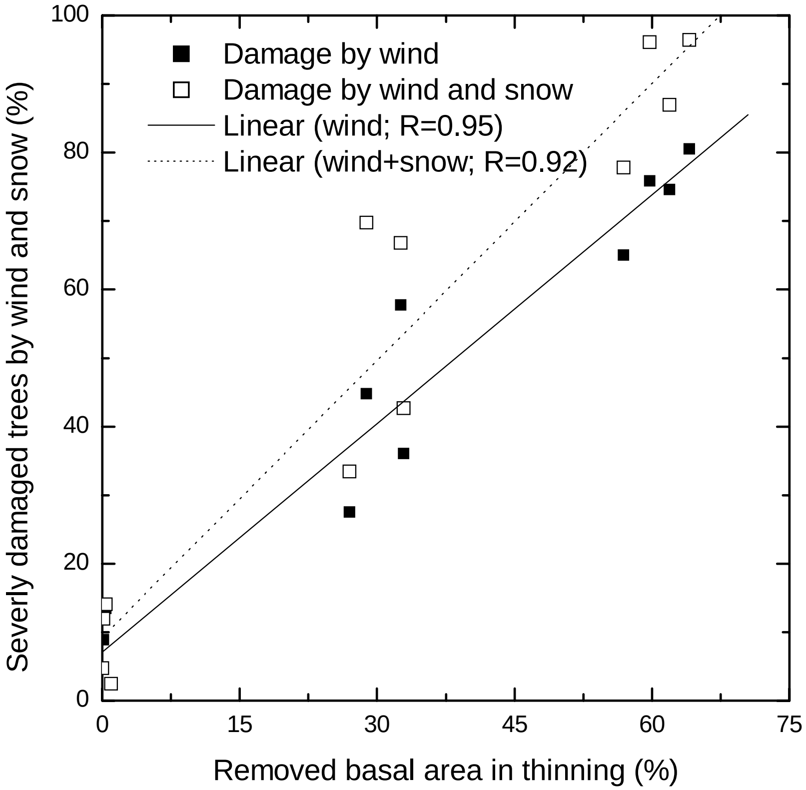

Figure 2. Damage by wind and snow in relation to removed basal area in thinning (%) three years prior to the storm.

Clear differences in the types of storm damage sustained in the normally thinned plots compared to the heavily thinned plots appeared. The amount of stem breakage was almost negligible in the former (less than 5%) while 24-50% of the stems were broken (mean, 36%) in the latter.

In the combined spacing and thinning experiment the percentage of wind damaged trees varied from 6-26% in the different treatments. The highest damage level was recorded in 3 m spacing with thinning from above. It was indicated that thinning from below had lower injury levels than thinning from above. In 2 m spacing, 6.7- and 12.7% of the trees were damaged in thinning from below and above respectively. Corresponding values in 2.5 m spacing was 6.2- and 11.5%. The percentage of damaged trees in the unthinned plots (3 m spacing) was 7.8%.

It has been reported that trees with strongly tapering stems are more stable than less tapered trees (Prpić 1969; Cremer *et al.* 1982; Valinger & Fridman, 1997). This was confirmed in the thinning experiment (paper II and III). Since additional diameter measurements were conducted at 6 m stem height on sample trees it was possible to correlate stem taper between 1.3 and 6 m with damage risk. This was done only in the normally thinned plots (in total 67 trees). All 67 trees were regarded as independent observations. High tapers were found to be associated with low risks for storm injuries and low total (snow and wind) damage risks. The mean taper for damaged and un-damaged trees (only wind damages) was 0.73- and 0.83 mm m^{-1} respectively (p=0.025). The corresponding values including snow injuries were 0.73 and 0.84 mm m^{-1} (p=0.012). Since larger trees had a higher stem taper the connection between damage resistance and tree form may be hypothetically related to the trees' size instead of their taper. This hypothesis was valid to some extent, but since the ratios between the mean diameters of damaged and undamaged trees were 0.99 after the storm, and 0.96 after accounting for damage caused by both the storm and snowfall, the effect of tree size on damage seems to be minor. Stem taper between breast height and 6 m stem height was a better predictor of storm damage than the often used height to diameter ratio (H/D-value). The H/D value (only wind damages) for damaged and un-damaged trees was 95 and 91 but the difference was not significant (p=0.213).

The injured trees in normally thinned and unthinned plots were re-measured one and two growing seasons after the storm and snow injuries were recorded (the heavily thinned stands were excluded from the comparison). The basal areas in all plots were further diminished by sampling trees for the biomass analyses. The basal area level in autumn 2004 and at the start of the growing season in 2005, after injuries and cutting, on each previously unthinned or moderately thinned plot together with the basal area and volume growth during 2005 and 2006 are shown in table 4. The volume growth in 2005 and 2006 was estimated as follows. I assumed that the changes in form height following each treatment during 2005 and 2006 were the same as in the growing season prior to storm felling, and then calculated the stem volume growth using the formula:

$$V = BA \times \Delta FH + FH \times \Delta BA + \Delta FH \times \Delta BA$$

Where: V is volume, BA is basal area under bark and FH is form height.

The basal area in the buffer zone after damages and cuttings (see Paper II and III for details) compared to the net plot was on average 3.5% higher in the control plots and 19.8% higher in the moderately thinned plots. Volume growth in the control plots was clearly lower during the two years following the heavy storm in winter 2005 than in the preceding years. The heavy drop in volume growth in the normally thinned plots (compare data in table 2 and figure 2 in Paper II with Table 4 in this thesis) is not surprising, but it should be noted that the rapid growth recovery observed in the first two growing seasons following the thinning in 2002 was not repeated following the storm-induced reduction in stem numbers.

Table 4. Basal areas at the start of the growing season in 2005 and both basal areas and volume production in 2005 and 2006.

Treatment	plot	Basal area in Autumn 2004 (m^2/ha)	Basal area in Spring 2005 (m^2/ha)	Basal area growth during 2005 (m^2/ha)	Volume growth during 2005 (m3/ha)	Basal area growth during 2006 (m^2/ha)	Volume growth during 2006 (m3/ha)
Unthinned	11	34.2	30.5	0.66	9.4	0.73	10.1
Unthinned	21	35.0	33.0	0.45	8.1	0.66	9.9
Unthinned	31	37.7	29.0	0.83	10.5	0.73	9.9
Unthinned	41	35.0	27.2	0.83	10.2	0.80	10.2
Normally thinned	12	26.9	14.7	0.65	8.3	0.64	8.6
Normally Thinned	22	27.0	13.3	0.67	8.3	0.69	8.7
Normally thinned	32	28.2	7.8	0.41	5.0	0.42	5.3
Normally thinned	42	27.5	6.0	0.21	3.0	0.29	3.8

Compared to the control plots the volume growth in the normally thinned plots averaged 66% in the first growing season after the storm and 67% in the second. The decreased volume growth in the control plots in 2005 and 2006 could be attributed to reductions in basal area and clustered stem losses, unfavourable climatic conditions and/or storm-injuries to roots. The climatic conditions during the two years following the storm were less favourable than average due to low precipitation (Ulf Johansson, pers. comm..), but it seems reasonable to assume that the growth reduction in the control plots was to some extent related to root injuries and storm recovery. The presence of a negative growth effect due to storm-induced root damage is also supported by the lack of a thinning response in normally thinned plots compared to unthinned controls in 2005 and 2006.

Paper IV

In Sweden, mechanisation of forestry activities began in the 1950s and although the machines were initially mostly used in clear cuttings they were later used in thinnings as well. Disturbance by the machinery used in thinnings increased the amount of injuries to the stems and coarse roots of remaining trees and numerous thinning systems were evaluated in terms of this risk during the 1970s and 1980s. However, apart from for a country-wide investigation conducted by the National Board of Forestry in 1997 (Anon. 1998), the only large-scale survey in which injuries to stem and coarse roots after thinning with a cut-to-length system using harvesters and forwarders were assessed was performed in the late 1980s (Fröding, 1992). No large-scale surveys focused entirely on Norway spruce stands.

The aims of the study reported in Paper IV were to estimate the injury levels to stem and coarse roots of remaining trees after thinning with a cut-to-length system using harvesters and forwarders in even-aged Norway spruce plantations in southern Sweden and to investigate correlations between injury levels, stand parameters, thinning season and the machinery used. Furthermore, the importance of machinery-related injuries with respect to risks for rot infection and reductions in quality was assessed in a literature review.

Materials and methods

The stands investigated in this study were stands that had been thinned in routine operations in southern Sweden, randomly selected from forestry company databases. The material was divided into stands that had been subjected to early and late thinnings, the former defined as a thinning in which strip-roads were established. The total number of stands in the study was 33, 21 of which had been subjected to early thinnings and 12 to late thinnings. All of the stands were situated on fertile sites. Data on each stand were collected in a sample plot survey. Each sample plot started from one edge of one strip-road and extended across it, perpendicular to the direction of the road, into the forest either to the edge of the next strip road or the edge of the stand, if there were no intervening roads. The widths of the plots were always 10 m.

In order to detect all injuries the slash material in each plot was removed. An injury was defined as removal of the bark and cambial layer, exposing the sapwood. Injuries to coarse roots situated further than 70 cm from the stem and to roots smaller than 2 cm in diameter were not counted. The injury frequency was presented as the percentage of trees with injuries relative to the total number of trees left after thinning. Since injuries smaller then 15 cm^2 are disregarded in inventories by the Swedish National Board of Forestry we calculated frequencies of both all injuries and injuries larger than 15 cm^2.

Silvicultural data, such as the basal area and number of stems before and after thinning, thinning quotient etc. were collected in the forest and additional information on machinery mass and thinning season were given by the forestry companies or contractors.

Results

In the early and late thinned stands, the total injury levels were 9.8% and 14.8%, respectively, while the corresponding frequencies for injuries larger than 15cm^2 were 5.8 and 10.8%. The difference in injury frequencies between early and late thinnings was due to significantly higher frequencies of root injuries following the latter. The injury level was significantly higher amongst trees adjacent to strip roads compared to trees in the interior of the stand. Most of the injuries were small, and the total injured area in trees with stem injuries averaged 30 to 40 cm^2, regardless of whether they were in early or late thinned stands. Corresponding values for root injuries were 70 and 110 cm^2, respectively.

Previously unthinned stands with high initial stem numbers and large basal areas were at higher risk of injury in the thinning operation. Thinning during winter reduced the amount of root injuries in early thinnings. Stem injuries in late thinnings were significantly negatively correlated to the width of the strip roads.

Discussion

Combination of initial spacing and thinning regime

Numerous studies, including paper I, have shown that increased initial spacing results in trees with larger breast height diameters and larger knots (Sjolte-Jørgensen, 1967; Handler & Jakobsen, 1986, Johansson, 1992). It is also well known that other quality variables (stem cracks, basic density) are related to growth rates early in the rotation period (Persson, 1985; Johansson, 1997). At a given diameter at final cut, increased growth when the stand was young gives a larger proportion of juvenile wood in the bottom log (Pape, 1999c) and juvenile wood is undesired for different kinds of end uses (Danborg, 1994a; Brolin, Norén & Ståhl, 1995; Forsberg & Warensjö, 2001). Hence, decreasing the mean diameter in thinning might be an important measure for improving stand quality.

Diameters in the stand are inevitably lower after thinning from above than after thinning from below, by definition. The scope to increase the timber quality by thinning from above in sparse stands is dependent on the correlations between different quality traits, diameter at breast height, the diameter distribution and spatial distribution of large trees (*c.f.* Persson, 1975a, Johansson, 1992; Klang, Agestam & Ekö, 2000). The results of paper I showed that it is possible to achieve similar quality in the remaining stand with 3 m initial spacing and thinning from above as with 2 and 2.5 m initial spacings and thinning from below. However, this was to some extent related to the more intense first thinning in the sparse stands. The volume growth up to the time of first thinning was also higher in this study than expected from previous, larger-scale studies (Handler & Jacobsen, 1986, Pettersson, 1992, Fahlvik & Nyström, 2006). Given a lower standing volume at the time of first thinning, there would have been less scope for improving stand quality by thinning from above. Quality traits with weak or negative correlations to DBH include (*inter alia*) double stems, spike knots and forks. Since those quality reducing-features, are usually related to injuries to the leading shoot, due to, for example frost, or game browsing (Bergqvist, 1998; Langvall, 2000) the competitive status of trees with such injuries may be adversely affected by asymmetric competition with their neighbours (Nilsson, 1993), and thus be more frequent in smaller than in large diameter classes (Pettersson, 2003).

Decreasing the initial spacing compared to standard would reduce establishment costs and could increase the net financial returns at first thinning since the trees would be larger, especially if thinning from above was applied. Such a silvicultural regime (wide initial spacing and thinning from above) seems to give acceptable quality in the stand left after thinning as long as the quality traits are strongly correlated to the diameter *per se* (*e.g.* branch diameter, density, juvenile wood content and stem straightness). Given the same thinning intensity in the first thinning the volume growth in even-aged young Norway spruce stands after thinning from above, or crown thinning, is reported to be equal to, or slightly inferior to, thinning from below (Carbonnier, 1954; Vuokila, 1960b; Hamilton, 1976; Vuokila, 1977; Schober, 1979, 1980, Eriksson & Karlsson, 1997). Furthermore, increasing the initial spacing reduces the risks for infection by root rot (Due, 1960, Venn & Solheim, 1994; Johansson & Pettersson, 1996) and damage by both snow (Braastad, 1979; Kramer, 1980) and heavy winds (Blackburn & Petty, 1988; MacCurrach, 1991; Gardiner & Quine, 2000). Use of increased initial spacing with fewer thinnings should also decrease the total amount of thinning injuries to stems and coarse roots during the rotation (Paper IV). However, a negative aspect of wide initial spacing is the decreased level of freedom for future silvicultural treatments, especially thinning programs, which also has adverse economic implications (Lohmander, 1992)

The most common damaging agent for planted Norway spruce in southern Sweden is the pine weevil (*Hylobius abietis* (L.)) (Petersson, 2004; Wallertz, 2005). The frequency of pine weevil damage could be predicted using information on the insecticides and/or mechanical agents, mechanical site preparation techniques and shelterwood that may have been applied (Petersson & Örlander, 2003). In almost all replanted clear-cut areas additional seedlings, originating from either advanced regeneration from previous rotations or newly naturally established seedlings, will be present (Tirén, 1949; Andersson, 1988; Karlsson, 2001). Frequencies of additional seedlings originating from natural regeneration (mainly birch) could also be modelled using information about the size of the regeneration area, seed sources on the clear-cut and in its vicinity, and site preparation methods that may have been applied (Karlsson, 2004). Hence, since both losses and gains of trees can be predicted, to some extent at least, regeneration treatments together with pre-commercial thinning should bee used as a unity in order to form the new stand. If Norway spruce is the desired species, additional natural regeneration may represent either an additional burden at the time of pre-commercial thinning or a measure to increase stocking and hence opportunities to improve volume production, wood quality and financial returns (Tham, 1988, Lohmander, 1992; Bergqvist, 1999; Valkonen & Valsta, 2001; Fällman & Nenzen, 2005; Agestam *et al*., 2006).). Since it has been shown that it is possible to grow birch and spruce together (Lindén, 2003; Fahlvik *et al*., 2005), and in many ecological respects this is preferable to cultivating pure monocultures of spruce (Thelin, 2000; Brandtberg, 2001), it seems reasonable to reduce the amount of planted trees per hectare at sites where high levels of seedlings could be predicted to establish naturally. Although care should be taken in any attempt to modify current silvicultural practices on the basis of the results presented in Paper I, they surely highlight the need to reconsider optimal initial spacings in relation to subsequent activities, such as pre-commercial thinning and thinning.

Thinning response

Since trees in a stand compete with each other for growth resources (light, water and nutrients) their individual growth is hampered. Thinning changes the competition and consequently the growth rate of the remaining trees. The thinning response could be defined as the difference in growth between a tree growing in a thinned stand and a tree of identical size and age, subject to identical competition from neighbours but growing in an unthinned stand (Pukkala, Miina & Kellomäki, 1998). According to Jonsson (1995) the thinning response could also be defined as "the difference between the actual growth and the growth that would have occurred if the forest had not been subjected to thinning". It is also important to define whether "growth" refers to increments at breast height, total stem volume growth or total production above or below ground (amount of assimilated carbon).

Thinning response of individual trees

The competition for light is obvious in a dense spruce forest on a fertile site. Initially after thinning the remaining trees will receive higher light levels in the lower parts of their crowns and hence increase their production (Ginn et al. 1991, Hale, 2001, 2003). The gaps created in the canopy by thinning (Johansson, 1986) are gradually filled through crown expansion of the remaining individual trees and the production rate of the trees is gradually increased. Since thinning responses have been recorded even in stands that are not limited by light (Varmola, Salminen & Timonen, 2004) decreased competition for nutrients and/or water may clearly also explain some of the thinning response by individual trees (Romell, 1938; Aussenac, 2000).

In the first growing season, the trees in the heavily thinned stands (Papers II & III) showed a moderate positive response to thinning (Figure 4. in Paper II and figure 4. in Paper III). If the enhanced growth rate at breast height was not a result of changes in resource allocation, as indicated solely by the observed stem form changes in the trees (Figure 2. in Paper III), this immediate response could probably be attributed to changes in light conditions in the lower part of the individual tree crowns. Since the amount of new needles is determined in the preceding year, the amount of new needles during the first growing season was not increased in the thinned stands. However, the needle litter fall per unit basal area was lower in the thinned compared to unthinned plots during the first year and therefore the tree crowns were slightly larger at the beginning of the second growing period. Due to the increased light levels throughout the crown, the new needles produced in the second and third growing seasons were probably sun needles, and hence for a given needle weight the canopy layer was more effective in the heavily thinned plots during the second and third growing seasons than in unthinned stands (Figure 3. in Paper III).

Decreased competition for water in the heavily thinned stands (Figure 5. in paper II) might also have allowed the trees to continue their growth for a longer time in dry periods than trees in the control plots (Lagergren, 2001; Misson,

Nicault & Guiot, 2003). However, this hypothesis was not supported by the band-dendrometers measurements (Figure 4. in Paper II).
Moisture, temperature, mineral concentrations, and gaseous atmospheres are primary effectors of root system development (Zobel, 1989). Increased soil water content has been shown to be positively related to root growth (Kätterer *et al*., 1995; Sword, Haywood & Andries, 1998) and even though the optimum temperature for root growth varies with the species and genotype, stage of development, and supply of soil moisture and oxygen (Kozlowski, Kramer & Pallardy, 1991), there is an increasing growth rate of roots with increasing soil temperature for the temperature range most common in nemoral and boreal forests (Teskey & Hinkley, 1981; Lahti *et al*., 2005).

Expansion of the root system together with an increased amount of inorganic nitrogen in the soil and higher mineralization rates (in the strip roads) lead to higher uptake rates of nutrients, which in turn induce crown expansion and hence growth. It is also possible that increased amounts of soluble inorganic nitrogen released in the root zone, especially for trees adjacent to strip roads, decreases their need for expansion of the root system and hence their allocation of biomass to stem wood could be enhanced. It has been argued that increased amounts of nutrients should reduce the need for fine root growth and increase allocation to shoot growth (Cannell, 1989; Sheriff, 1996, Bartelink, 1998). However, this hypothesis, that biomass accumulation favour shoots when trees are grown with high resource availability, was rejected in a study by Coyle & Coleman (2005). The few studies that have investigated allocation to fine roots after thinning suggest that the roots act as a similar or even stronger sink for fixed carbon then before thinning (Santantonio & Santantonio, 1987a, 1987b; Beets & Whitehead, 1996, López, Sabate & Gracia, 2003).

The competition between trees in a stand may be either symmetric (two-sided) or asymmetric (one-sided). Symmetric competition means that all trees grow in relation to their size and asymmetric competition means that the growth of large trees is only slightly affected, or not affected at all, by small trees, while the growth rates of the smaller trees is slower than expected from their size alone (Cannell, Rothery & Ford, 1984; Weiner & Thomas, 1986; Firbank & Watkinson, 1987). The asymmetry of competition increases when the main limiting growth factor is light, while symmetric competition generally occurs on sites limited by water and/or nutrients (Nilsson, 1993). It was argued in Paper III that the response to thinning of the largest trees in the heavily thinned stands implies that the post-thinning growth of intermediate and small individual trees was not entirely limited by their competition for light. This conclusion was further supported by the data on the growth reactions of the trees adjacent to strip-roads in the heavily thinned plots (Table 2 and Figure 3 in Paper II). The production per unit area in the strip-road zone was twice as high as further in the stand in the third year following thinning, mostly due probably to the increased availability of nitrogen from the harvesting residues left on the roads. It has been claimed that fertilization on sites with high site indices will have little or no effects on growth (Møller, Scharff & Dragstedt, 1969; Stone, 1986; Sikström *et al*., 1998) and the lack of response to fertilization observed in a large-scale thinning and fertilization experiment in spruce stands in southern and middle Sweden has also been attributed to this (Eriksson & Karlsson, 1997, Eriksson, 2006). However it has been shown that nutrient optimization (mainly added nitrogen) in young Norway spruce stands on sites with high site indices in southern Sweden has resulted in a 60% increase of production per unit area (Bergh et al., 1999; Bergh & Linder, 2006). Taken together, the results from Bergh et al. (1999), Eriksson & Karlsson (1997), Eriksson (2006) and Paper II indicate that increasing the amount of nutrients (nitrogen) in stands with low leaf area indices increases the production per unit area simply by increasing the rate of LAI (or crown) expansion.

Thinning response at stand level

Although most long-term thinning experiments have found small differences between actively thinned and unthinned stands (Table 1) numerous investigations have shown that thinning in young stands could stimulate the volume production per unit area in the first 5-15 years after thinning (Table 3., see also Pretzsch, 2004; Judovalkis, Kairiukstis & Vasiliauskas, 2005). However, short-term thinning reactions at stand level must be negative since the canopy layer in the stand must either increase in size, effectiveness, or both, before growth can be increased. The initial decrease and subsequent recovery of LAI over time after thinning is of great interest. However, after canopy closure, neither the basal area reduction after thinning and light transmittance (Hale 2001, 2003), nor the relationship between decreasing LAI and decreasing light absorbance is linear (Linder 1985; Long & Smith 1992). Thus, even without any growth response in LAI in thinned stands, the losses in volume production will be smaller than the proportion of needle biomass lost due to increased irradiance of needles that were previously shaded (Ginn *et al.*, 1991; Peterson *et al.*, 1997). Intensive cutting will lead to production losses since the initial drop in needle biomass must at least partly recover to pre-thinning levels before volume production can recover.

Bradley (1963) hypothesised (and showed with data from a thinning experiment in Corsican pine) that the short-term drop in volume production following thinning is subsequently compensated for by increased production per unit area compared to unthinned control plots. This growth pattern, an initial drop followed by a peak that levels out during the first 5-10 years after thinning (Figure 3), is supported by data reported by Lynch (1980) on the basal area production per unit area during the first six years following thinning, and to some extent by the results in Paper II, although the total production per unit area was only followed for three years. The growth was already higher in the third growing season, albeit not statistically significantly higher, in the heavily thinned plots compared to the unthinned controls.

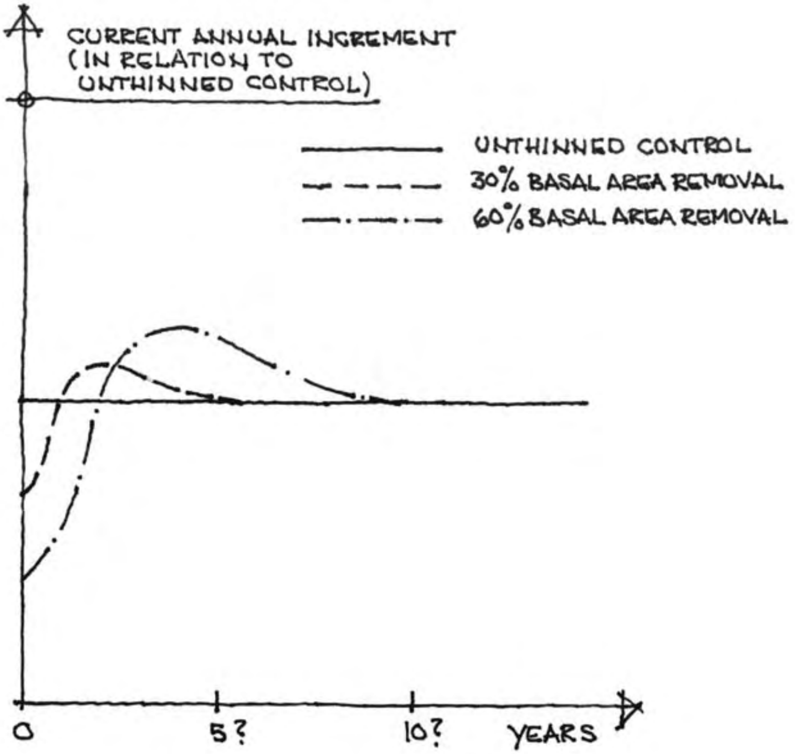

Figure 3. Hypothesised pattern of current annual increment in the first five to ten years after thinning of different grades (freely after Bradley, 1963).

The increased production per unit area at short- or intermediate time scales has been called “Wuchsbeschleunigung” or “growth quickening effect” (Dittmar, 1959; Assmann, 1961, 1970). How is it then possible that removal of a certain amount of effective members from a tree population leads to increased growth per unit area? The increase of individual trees can be explained by reduced competition for growth resources, but what about increases in production per unit area? It could be argued that the increased amount of nutrients from harvesting residues is a resource that is used to rebuild the production “equipment” (roots and needles) to post-thinning levels rather than to increase production per unit area. However, as long as thinning is carried out from below, the needles destined to become harvesting residues will have been accumulated over a long time on trees with small production capacities. The needles on each tree have developed over approximately five years, and this nitrogen resource is supplied as harvesting residues and released over a shorter time than it was accumulated, together with nitrogen release from decomposition of fine roots, then used to produce sun needles on trees in improved light conditions. Furthermore, there may be a surplus of growth resources resulting from increased soil activity, and hence release of inorganic nitrogen bound in the soil due to increases in soil temperature and moisture (Bornebusch, 1930; Wright, 1957; Aussenac, 2000; Øyen, 2001).

In addition to this physiological explanation of the thinning reaction in terms of volume growth per unit area, a further effect is provided by stem selection in the thinning (Assmann, 1970, Elfving, 1985). However, evaluating the selection effect is not straightforward. The competitive status of a tree has both genetic components and components related to differences in micro-site conditions and small-scale calamities (browsing, frost, fungi infections) affecting the tree in question or its neighbours. Selection of the genetically superior producers implies thinning that strictly removes the smallest trees. It is of course possible that some small trees have better growth-related genetic traits than neighbouring large trees, but are situated on less fertile micro-sites or have been damaged by browsing or frost, but it is difficult or impossible to distinguish such trees from those that are genetically inferior during a thinning. The other possibility for increasing growth after thinning through selection is to look for trees showing “bad growth”, i.e. trees that are descending in diameter rankings, this is to a large extent dependent on the health status (or adverse changes in the health status of a tree’s closest neighbours). If it is possible to identify trees that are decreasing in the rankings there will be scope for a positive selection effect.

To summarize; a lower growth reduction compared to the amount of volume removed could be explained by the following considerations:

1. Removal of a certain needle mass (or basal area) does not imply a linear reduction in capacity to intercept light.
2. Leaving harvesting residues in the stand after removing trees will result in a rapid increase in available nitrogen, which may increase needle efficiency. Increases in soil microbial activities and the release of tightly bound inorganic nitrogen could further enhance this effect.
3. Improved water status of the soil may allow the remaining trees to grow longer during dry periods.
4. If the trees removed in thinning account for a higher proportion of the total standing volume than the proportion of total production for a few years prior to thinning then the selection effect will be positive.

The “Wuchsbeschleunigung” or “growth quickening effect” might therefore be explained as a short-lived phenomenon in cases where the positive effects of increased nutrient status exceed the initial growth reduction.

Risks and calamities

The main implication of the results presented in Paper I, II and III, together with previous reports concerned with production related to initial spacing and thinning in even-aged Norway spruce plantations is that there is a large “window of opportunity” for silvicultural regimes in terms of their effects on total volume production. For different possible thinning programmes this “window of opportunity" includes choices regarding thinning intensity and form, time of first thinning, geometrical pattern and number of thinnings or thinning interval (Carbonnier, 1966; Bryndum, 1978; Eriksson & Karlsson, 1997, Pretzsch, 2004, Mäkinen, Isomäki & Hongisto, 2006). The practical implications of this large "biological window" are that the silvicultural regime applied to Norway spruce stands should not focus on volume production but on the present, and predicted, economic situation and risks. A sound economically-based silvicultural regime for even-aged plantations of Norway spruce should ideally incorporate: low initial investment costs for all measures (including soil preparation, planting and pre-commercial thinning); satisfactory volume production; low risks for root rot, thinning injuries to stems and coarse roots, storm and snow damage, and mortality due to self-thinning; and production of large, high quality stems. However, optimal conditions for any one of these features will be far from optimal for others. Therefore, silvicultural planning must define and balance conflicting goals.

Thinning injuries

Paper IV in this thesis shows that thinning has a negative impact on the remaining stand due to a large amount of injuries to stems and coarse roots. Given the mean injury levels detected, and a thinning program, starting with 2500 stem ha^{-1}, with three thinnings in each of which 30% of the basal area is removed (random cutting of previously injured trees), the percentage of trees with injuries larger than 15 cm^2 at final felling would be 27%. Based on available literature concerning rot establishment and growth in various kinds of injuries it was proposed in Paper IV that 1-4% of the trees in the final felling will have been affected by advanced decay due to such injuries. Additional quality losses from healed wounds and staining should also be expected. However, the scientific literature regarding risks for infections in stem and root wounds is problematic to evaluate, for several reasons.

Firstly, how relevant are reported infection levels for different geographical locations to conditions in southern Sweden? Previous investigations on infection rate in thinning injuries in Sweden were limited to the central part of the country and almost solely focused on infections in root wounds (Nilsson & Hyppel, 1968, Lundeberg, 1972). Older Swedish literature also dealt with blazing wounds from practical timber marking (in central or northern part of the country) but those damages were generally larger and deeper than thinning wounds (Ernberg, 1907; Nordfors, 1923; Ekbom, 1928; Silvén, 1944). Vasiliauskas, Stenlid & Johansson (1996), Vasiliauskas & Stenlid (1998) and Vasiliauskas (1998) showed that risks for fungal infections of game wounds and the fungal flora in the wounds were quite similar in central Sweden and Lithuania, so since most studies in northern and middle Europe have found *Stereum sanguinolentum* to be the most important wound invader it seems reasonable to consider as many investigations as possible from Europe in attempts to estimate lower and upper limits for invasion frequencies of the types of wounds considered in Paper IV.

A second problem is related to the fact that in studies of risks for infection and spread of rot fungi in wounds of different sizes there is usually little knowledge about the sizes of the initial wounds. Koch & Thongjiem (1989) found that the sizes of small original wounds (8-100 cm^2) were increased by 555 % after 2.5 years, because of bark necrosis surrounding the initially exposed wood. Hence, it is possible that reported infection levels have been substantially underestimated in numerous investigations, especially for small injuries. However, we know that small injuries, to both stems and coarse roots, heal quite quickly and further fungal development then ceases.

The negative impact on the residual stand and future income of the injuries is not so great that radical changes should be made to a silvicultural system that has other substantial advantages (Boström, 1978; Kallio 1984), but it is always advisable to minimize their abundance.

Root- and butt rot caused by Heterobasidion spp.

Although they were not investigated in the studies this thesis is based upon, assessments of thinning in Norway spruce stands in southern Sweden should always consider the risks for introducing and increasing the spread of root rot (*Heterobasidion spp.*) associated with thinning activities (Vollbrecht & Agestam, 1995; Berglund, 2005). Both the number of thinnings and the thinning intensity are related to the spread of butt rot (Vollbrecht, 1994), but it would be of great practical value to know whether the overall risk for spreading root rot, given the same periodic mean basal area, is highest with one early heavy thinning or with a more frequent thinning schedule in which smaller amounts of basal area are removed in each thinning. Theoretically, the probabilities that thinnings will be sub-optimal, and introduce root rot, will be greater with a frequent-thinning schedule than with a single thinning, and there will also be greater scope to apply measures for preventing *Heterobasidion spp.* infection either by using protective agents (Berglund, 2005) or by thinning in winter (Brandtberg, Johansson & Seeger, 1996) with a single thinning.

Damages due to heavy winds and snow

The strong relationship between thinning grade and storm and snow damage observed in the thinning experiment reported in Papers II and III has been previously documented in Norway spruce stands and stands dominated by other tree species, both in Sweden (Persson 1972, 1975b) and abroad (Cremer *et al.* 1982, Lohmander & Helles 1987). It is also well known that recently thinned stands are most sensitive to storm injuries (Persson 1975b, Laiho 1987, Lohmander & Helles 1987).

Persson (1972) investigated a newly established thinning experiment in Norway spruce with seven different blocks located in different parts of southern Sweden that suffered heavy storms in either 1967 or 1969, for up to three growing seasons after thinning. In the treatments with thinning from below, the thinning grades ranged from unthinned controls to 70% removal of basal area with intermediate thinning grades of 20% and 40%. The plots in which 70% of the basal area was removed lost a further 21% of their remaining basal area in the storms, while the losses following the 0 to 40% thinning treatments were less then 1%. Injuries due to wet snow showed an opposite tendency, with injury frequencies being lowest following the heaviest thinnings. The cited author concluded that there was an inverse correlation (albeit very weak) between snow injuries and thinning intensity.

The general relationship between thinning intensity and risks for snow damages is not as clear as for storm injuries. Unthinned stands are generally believed to be at higher risk for snow injuries than thinned stands. However, in the first years after thinning even snow injuries are reported to be more frequent in thinned compared to unthinned stands.

It is important to consider the total injury level over a whole rotation period, and to adjust all silvicultural options accordingly to find the best combination of reduced risks and satisfactory production of desired forest products (Persson, 1975b; Cameron, 2002; Gardiner *et al.*, 2005). In even-aged Norway spruce plantations in southern Sweden subjected to different thinning regimes, the total amount of damage from both wind and snow during a 25-year period was highest in unthinned stands, although the between-treatment differences were not significant according to a study by Valinger & Pettersson (1996). Investigations from the same experimental series reported by Valinger & Pettersson, (1996) after the heavy storm that affected southern Sweden on the night between the 8th and 9th of January 2005 detected no statistically significant differences in damage rates related to different thinning programmes, amongst either spruce or pine stands (Valinger *et al.*, 2006). Over a longer time period the unthinned stands may also sustain as high levels of snow and wind injuries as heavily thinned stands, and additional losses from self-thinning are more frequent in dense stands. It is also important to consider variation in damage occurrence due to geographic location, topography and site conditions (Valinger & Fridman, 1999; Kuboyama & Oka 2000; Zhu *et al.* 2006; Olofsson, 2006).

To minimize damage due to snow and heavy winds in a silvicultural system that includes cuttings, pre-commercial thinning (provided it is done well) can enhance subsequent stand stability, and thus help minimize damage due to snow and heavy winds later in the rotation period (Anon, 1969; Nielsen *et al.*, 2004; Achim, Ruel & Gardiner, 2005). Reduced competition between individual trees in early phases of stand development increases root growth and hence the stand stability over the whole rotation period (Nielsen, 2001; Nielsen et al., 2004). The earlier the cuttings, the shorter the time the stand will start to recover pre-cutting levels of stability (Sjöström, 1932; Nielsen, 2001) and the greater the stand stability will be (Jacobs, 1936; Werner & Årmann, 1955; Hütte, 1970; Kramer, 1979; Cameron, 1982; Rössler, 2006). Cutting in an old, dense and previously unthinned stand will be most hazardous (Sjöström, 1932; Jacobs, 1936; Anon., 1954; Persson, 1975b; Abetz & Unfried, 1984; Chroust, 1987; Nielsen 2001). Nielsen (1990) claims that in order to obtain a stable stand with a flexible rotation length, the number of trees at 6 m height should not be higher than 2,000-3,500 stems per hectare and no thinning should be applied in the expected last third of the rotation period. Delaying the first thinning, in order to increase the volume of merchantable volume and dimension of individual trees (Huuskonen & Hynynen, 2006) and hence the economic returns (Valsta, 1992; Pukkala *et al*., 1998; Hyytiäinen & Tahvonen, 2002), will enhance the risk of wind damages.

Practical implications

A silvicultural system with wide initial spacing and no thinning will be preferable to minimise risks for storm felling, injuries from logging machines (obviously since no thinning is carried out) and butt rot. However, this system will be less favourable in other respects since timber quality and production are likely to be lower and there will be no income before final felling. A silvicultural system with wide initial spacing and thinning from above might combine the advantages of sparse stands with the avoidance of losses from a no-thinning regime. Most stands at thinning age are also too dense for application of a non-thinning system since dense stands are sensitive to snow injuries (Hesselman, 1912; Schotte 1916; Chroust, 1987) and additional losses from self thinning (Hynynen, 1993; Eriksson & Karlsson, 1997, Skovsgaard, 1997). Given the need for thinning, the thinning regimes with the lowest overall negative associations with root rot, stem and root injuries and damage due to wind and snow seem to be regimes with early and heavy thinnings. Early and heavy thinnings should also be preferable in stands with large variation in timber quality. In these stands trees of lower quality should be removed to favour the trees of better quality as early as possible. However, heavy thinnings might results in large variation in annual ring width and increased spiral grain (Danborg, 1994b; Pape, 1999d; Säll, 2002). Additionally, early thinnings with high grades and intensities will reduce the freedom to choose between different thinning programmes later in the rotation.

Further research

The initial area volume growth response after thinning with different grades needs further study. The theoretical figure (Figure 3.) initially presented by Bradley (1963), should be investigated in field experiments. Investigations on volume production per unit area in each year following thinning at different intensities should not be evaluated by standard volume functions, so such investigations should include destructive sampling at the end of the period of interest (approximately 10 years) or alternatively be based on volume measurements of standing trees at regular intervals.

For practical foresters the findings that initial spacing and thinning grade in young even-aged stand of Norway spruce does not have a major affects on total volume production seen over a whole rotation are of great practical value. However, there is limited knowledge about the effects of differences in thinning grades applied at later stages in the rotation period, and more specifically how intense cuttings can be applied without causing significant growth losses.

The strong response of trees adjacent to strip roads after thinning observed in the studies reported in Papers II and III suggests that additional nutrient (nitrogen) supply might increase growth even on sites with high site indices. This conflicts with results from experiments in which the effects of combinations of thinning and fertilization were examined in Sweden (Eriksson & Karlsson, 1997; Eriksson, 2006). However, the lack of a nitrogen response observed in the cited studies may have been due to limited removals in each cutting. There is a need for more knowledge about growth responses to fertilization in combination with heavy thinnings. It is also important to evaluate wind damage in such experiments since the combination of fertilization and heavy thinning increase such damage (Laiho, 1987; Valinger & Lundqvist, 1992).

The Nordic and European literature concerning rot infection in thinning injuries on Norway spruce is complicated to evaluate. Investigations of the effects of small injuries, up to 50 cm^2, both on coarse roots and stems, on timber quality and risk for rot infection is absent in southern Sweden and needs to be examined.

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