Growth Allocation and Stand Structure in Norway spruce Stands

Expected taper and diameter distribution in stands subjected to different thinning regimes

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Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2005

Acta Universitatis Agriculturae Sueciae
2005:75

Abstract

Karlsson, K. 2005. Growth allocation and stand structure in Norway spruce stands. - Expected taper and diameter distribution in stands subjected to different thinning regimes. Doctor's dissertation. ISSN 1652-6880. ISBN 91-576-6974-0.

This thesis is based on analyses of permanent sample plot data gathered over periods of 10-34 years from an experiment in which a wide range of thinning regimes, and thinnings combined with N-fertilisation, were applied to 25 even-aged Norway spruce (*Picea abies* (L.) Karst.) stands in southern Sweden (56-63 N^o). At the start of the experiment, before the first thinning, the dominant height was 12-18 m. The overall objective was to evaluate the extent to which growth allocation along the bole and the stand structure of *Picea abies* stands can be controlled by different silvicultural regimes. To do this the data were used in four studies to evaluate the impact of: thinning and N-fertilisation on stem form and taper (Study I); different thinning regimes on the removal and growth in the diameter at breast height (DBH) of individual stems (Studies II and III); and the thinning regimes on the growth in mean DBH of four classes of the largest stems by DBH ha^{-1} (Study IV). The studies *(ii)* and *(iii)* form a growth model. In stands subjected to different thinning regimes, one model predicts which individual trees will remain at future points in time and an associated model predicts the future DBH of the remaining stems. Separate models were developed for stands thinned from below, stands thinned from above and unthinned stands. In Study IV the actual and genuine increases in the arithmetic mean DBH of the 100, 200, 300 and 400 largest stems by DBH ha^{-1} associated with six different thinning regimes in periods up to 35 years were compared to the corresponding stems in unthinned stands.

 The goals of achieving rapid diameter growth and low stem tapering cannot be attained simultaneously as heavy thinnings cause increased tapering, and thus silvicultural regimes must reflect a compromise between these and other production objectives. Trees in thinned and N-fertilised stands had the same taper as trees in equally thinned, unfertilised stands. Heavy thinnings from below promote high frequencies of thick stems and extra heavy thinnings promote high frequencies of extra thick stems. Thinning from above (or no thinnngs) may be an alternative to thinning from below in situations where a main crop consisting of moderately thick stems would be regarded as a satisfactory outcome. The actual mean DBH of larger stems can be increased, compared to the corresponding stems in unthinned stands, by up to 2.6 mm per year if extra heavy thinnings are carried out. The biological response to thinning of thick stems is influenced by the thinning intensity but not by the thinning method. The variation in DBH increases over time but increases more in stands thinned from above and unthinned stands than in stands thinned from below.
Key words: DBH distribution, DBH increase, growth simulator, mortality, *Picea abies,* stem form, stem taper, taper changes, thinning.

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Appendix

Papers I-IV

The thesis is based on the following papers, which are referred to in the text by the corresponding Roman numerals:

I.   Karlsson K. 2000. Stem form and taper changes after thinning and nitrogen fertilisation in *Picea abies* and *Pinus sylvestris* stands. *Scandinavian Journal of Forest Research* 15: 621-632.
     (The *Pinus sylvestris* part of Paper I is not discussed in the thesis)

II. Karlsson, K. & Norell, L. 2005. Modelling survival probability of individual trees in Norway spruce stands under different thinning regimes. *Canadian Journal of Forest Research* 35: 113-121.

III. Karlsson, K. & Norell, L. 2005. Predicting the future diameter of stems in Norway spruce stands subjected to different thinning regimes. *Canadian Journal of Forest Research* 35: 1331-1341.

IV. Karlsson K. 2005. The impact of the thinning regime on the mean diameter of the largest stems by DBH in even-aged Norway spruce (*Picea abies* (L.) Karst.) stands. *(Submitted)*

Papers I-III are reproduced with permission of the journals concerned.

Introduction

Background

Forest management decision-makers have a great need for reliable predictions regarding the ways that different silvicultural regimes are likely to affect stand development. Appropriate forest growth models can provide such forecasts (Pukkala et al. 1998). Such models can be categorised in several different ways. For instance, one can distinguish (*inter alia*) physiological, empirical (statistical), whole-stand, single-tree and diameter distribution models, etc. (Verma 1999). In addition there are also forest management modelling systems that operate on a larger scale than the stand level. Such models are used as support systems in strategic forestry planning at regional or company levels.

Physiological models

Physiological (or process-based) models are photosynthesis-based. The processes governing growth are well known and understood (Landsberg 1986, Landsberg & Gower 1997). Explanatory variables include (*inter alia*) foliage area, solar radiation, temperature, water and nutrition supply. Advantages of such models are that they can increase our understanding of factors that influence growth and they can easily be adapted to take account of changes in the environment. However, since growth processes are very complex and there is a lack of detailed knowledge about many of them, physiological models have not been commonly applied in forestry. Furthermore, physiological models normally yield estimates of total biomass production per unit area, and foresters are generally more interested in stand and single tree volume yields. Matala et al. (2003) have compared the outcome of a physiological versus an empirical (statistical) model designed for Scots pine, Norway spruce and silver birch stands. The models agreed well I terms of relative growth rates, especially in unmanaged stands. The statistical model was found to be quite stable in its predictions and not as sensitive to initial stand conditions and management as the physiological was.

Ecological models

Ecological (succession or gap) models are used to test ecological population theories. The models may be used to simulate tree population dynamics under different climatic management scenarios (Lindner et al 2000). Burgmann et al. (1996) have compared 13 different gap models' structure and behaviour. They concluded that *(i)* the models are quite sensitive to the formulation of climatic factors under current conditions, and this sensitivity is even more pronounced under a changed climate, *(ii)* adaptations of forest gap models to specific regions often have required more detailed sub-models of specific history, thus complicating model comparison, *(iii)* some of the complex models developed for region-specific applications can be simplified without hampering the realism with which they simulate specific compositions and *(iv)* attempts to apply the models

without modification beyond the area for which they have been developed have produced controversial results.

Empirical models

Most silvicultural models in current use are empirical models, i.e. models derived by observing, recording and generalising how forest stands react to different treatments. Survey data and data from permanent sample plots may be used in their construction. Growth functions are fitted to available data based on biological assumptions concerning the strength and direction (positive or negative) of variables that are likely to influence the growth of the stand. Such models will often give good estimates of expected growth, as long as the predictions are within the scope of the data used in their construction, but they may give uncertain estimates for predictions outside the range of the data set. Furthermore, since the models are based on historical data there is a risk that the outcome will become increasingly uncertain if the environment changes.

Empirical stand growth models can be categorised into three types, *(i)* individual tree models, which can be further divided into distance-dependent and distance-independent models *(ii)* diameter distribution models and *(iii)* whole stand models, (Verma 1999). Foresters are generally interested in both stand volume growth and the way the volume is distributed amongst different tree sizes. A commonly used general measure of tree size is the diameter at breast height (DBH). Diameter distribution models and individual tree models provide direct estimates of future tree sizes. For whole stand models, the future DBH distribution can be derived from predicted stand attributes (see, for instance, Eriksson 1976).

Most empirical models assume initial data regarding a stand at about the time for the first thinning. Explanatory variables include stand and site factors such as DBH (individual tree models), basal area ha^{-1}, stand or tree age, number of stems ha^{-1}, quadratic mean DBH, site index, soil type, altitude, latitude and longitude. The growth for a 5-10 year period is estimated and stand data to be used as a starting point for the next prediction period can be calculated. At the start of a period thinnings can be simulated. By repeating the prediction (and thinning) procedure a sufficient number of times the stand development up to the end of the rotation period can be predicted.

A number of empirical models have been developed to predict the expected growth of forest stands. In Sweden most attention has focused on whole stand models to date. For instance, Ericsson (1976) developed a model predicting the growth of Norway spruce, Agestam (1985) one for mixed stands of Norway spruce, Scots pine and birch and Persson (1992) one for Scots pine. Ekö (1985) and Söderberg (1986) both developed models for native species in Sweden. Ekö's model was a whole stand model and Söderberg's was a distant-independent, single-tree model. Recently, two distance-independent, individual-tree growth models have been developed for central European species: PROGNAUS (Sterba et al. 2000) and SILVA (Pretzsch et al. 2002). Söderbergh and Ledermann (2003)

have reviewed individual-tree growth simulators in Europe. For North American species and conditions a number of models are available, e.g. a stand-based growth and yield simulator for coastal Douglas fir (DFSIM) (Curtis et al. 1981, Fight et al. 1984) and Prognosis[BC], an adaptation of the U.S. Forest Service Forest Vegetation Simulator (FVS), applicable to forest species in British Columbia (Wykoff 1990).

Hybrid models

Hybrid models may combine features of both empirical and process-based models. Mäkälä et al. (2000) hypothesised that combining empirical information with the flexibility and strength of process-based models would be advantageous, while Landsberg (2003) asserted that the future of forest modelling must lie in developing hybrid models that use process-based functions to predict productivity combined with statistical descriptions of stand structure. FORECAST, developed in Canada, is an ecosystem-based, stand-level forest growth simulator that uses a hybrid approach in which local growth and yield data are combined with other data to estimate the rates of ecosystem processes related to the productivity and resource requirements of selected species. Details of FORECAST calibration and its application are provided in Kimmins et al. (1999) and Seely et al. (1999).

Deterministic and stochastic models

Irrespective of the model components a model may be deterministic or stochastic. Deterministic growth models provide estimates of the expected growth in the same way as means indicate expected outcomes. For a given initial stand and a given silvicultural regime a deterministic model always predicts the same result. However, any measure of the growth of forest stands may vary between years due to natural variations in the environment (Mäkinen et al. 2001, 2002, 2003, Johansson & Karlsson 2004). Therefore, stochastic models have been used to mimic the natural variation of outcomes by generating a range of predictions, each with a specific probability of occurrence. By repeating the prediction procedure with the same input data a sufficient number of times, stochastic models may indicate the natural variation and the risks associated with a particular silvicultural regime.

Removals

Removal of a tree in a stand may be due to any one of three types of causes: (*i*) regular natural mortality (non-catastrophic), (*ii*) irregular natural mortality (catastrophic) (Yang 1988) and (*iii*) active thinning. Accurate mortality or survival predictions are essential components of any stand growth model (Monserud 1976). Natural mortality is not very well understood (Hamilton 1986), and its irregular component is especially difficult to predict. However, one way to simplify the predictions involved is to predict the survival of trees – ignoring the reasons for removal (regular mortality, irregular mortality or active thinning) (Paper II).

Regular mortality (self-thinning) is induced by competition. Competition between neighbouring trees in a stand, both for below and above ground resources, is often considered to begin at crown closure (Ford 1982, Cannel et al. 1984). The competition reduces the size of the living crown and its capacity to produce the substrates needed to meet basic respiration requirements, and the ultimate outcome of competition is self-thinning. Self-thinning is not very well understood (Hamilton 1986), but the smallest trees are most likely to be removed in this process (Westoby 1984). The separation takes places relatively early in stand development (Harper 1977).

Irregular mortality (catastrophic mortality) – which is caused mainly by pests, snow and wind breakage – is very difficult to predict. Valinger & Petterson (1996) found that heavily thinned stands were most susceptible to damage caused by wind, especially a few years after a thinning. They also found that stands in which high numbers of trees were retained, e.g. stands thinned from above and unthinned stands, showed a higher proportion of snow damage, with suppressed trees being most threatened.

An individual thinning can be characterised by a combination of two measures: *(i)* the thinning intensity (TI), defined as the ratio of basal area (BA) of removed trees to total BA before thinning and *(ii)* the thinning quotient (TQ), defined as the ratio of the mean DBH of removed trees to the mean DBH of trees remaining in the stand. The outcome of each thinning can be adjusted by varying TI and TQ. (Papers II and III). Thinning programmes are composed of one or more individual thinnings, and both the number of thinnings and the period of time between them can be varied (Eriksson & Karlsson, 1997).

Stem versus stand growth

As long as the living space in a stand is not fully occupied, increases in stand density will be accompanied with increases in stand growth. If the living space can be fully occupied by fewer stems, the growth of individual stems will be promoted without loss of stand growth. Thinnings are generally believed to reduce stand growth and as TI increases more growth will be lost (Assman 1970). Norway spruce stands are known to be relatively lightly affected by increases in TI, and no marked reduction in the stand growth is likely to occur as long as the TI does not exceed 40 percent (Eriksson & Karlsson 1997). In such cases thinnings promote the individual stem growth without loss of stand growth.

Growth allocation and stem taper

The allocation of growth along the stem and the stem shape resulting from the growth pattern were important fields of study for forest botanists as early as the late nineteenth century. However, none of the many attempts to characterise stem shape mathematically has described the shape of stems with complete success. Much of the difficulty arises from the great variations in stem shape that occur among the trees in a stand, but a further complication is that the form and taper of

the stem of a single tree can differ considerably below and within the crown (Larson 1963).

Four general theories have been proposed to explain variations in stem shape, based on mechanistic, nutritional, water conduction, and hormonal processes (Larson 1963). The mechanistic theory states that the stem is shaped by adaptive processes that give it sufficient strength to withstand both the vertical forces exerted by the weight of the stem itself plus the weight of snow and ice that is likely to accumulate and (*ii*) the horizontal forces exerted by the wind that it is likely to encounter. The nutritional theory is based on the hypothesis that equilibrium is maintained between transpiration and assimilation. The amount of earlywood (conductive tissue) in the stem is determined by the rate of transpiration. Hence, trees with large crowns will produce strongly tapered stems with a high proportion of earlywood. The water conduction theory holds that the crown's needs for transpiration determine and regulate bole form since they can only be met by water conducted through the bole. The hormonal theory holds that bole form is dictated by hormonal interactions, since cambial activities are maintained by hormonal stimuli emanating from the crown and roots. Even though none of the four theories has been able to explain all of the variation in stem shape satisfactorily, a shared feature is that the allocation of growth is dependent on crown development. A tree's survival strategy under different environment conditions is stored in its genome and affects its growth allocation patterns. For example, increasing wind stress arising from thinnings will promote the allocation of more growth to the lower part of the stem and the root system (Valinger 1990, Telewski 1995). In contrast, it is more advantageous for a tree in an unthinned stand to allocate more growth to the upper parts of its stem and crown. It should be noted that a systems biology approach, incorporating all of the above mechanisms, may ultimately provide a fully satisfactory theory explaining variations in stem growth, but systems biology is currently in its infancy, and the tools required to handle the complexities involved have not yet been developed.

In the period between stand establishment and, roughly, the time of crown closure, juvenile trees in even-aged stands are free-growing, subject to a negligible degree of competition and have similar shapes (Muhairwe 1994). As the trees grow they begin to compete with each other, for both below and above ground site resources (Nilsson & Gemmel 1993). The intra-specific competition causes the living crown to recede by self-pruning and more growth to be allocated to upper parts of the stem, resulting in more cylindrical stems (Larson 1963). Thinnings reduce stand density, promoting increases in crown size, and more growth to be allocated to lower parts of the stem, i.e. thinnings cause stem shapes to be more conical (Larson 1963). Crown development is strongly dependent on stand density and, according to the general theories, trees with vigorous crowns will be strongly tapered, while trees with a long branch-free bole will be more cylindrical.

Implications of forest management

When choosing an appropriate silviculture regime a range of factors must be considered, since the thinning programme applied will affect a host of parameters, including the future wood quality (Pape 1999a, Pape 1999b, Pape 1999c), total production, amount of wasted production due to self-thinning (Eriksson & Karlsson 1997), breakage (Persson 1972, Valinger & Petterson 1996), the suitability of the stand for different end-products (Stevens & Barbour 2000) and harvesting costs (Lageson 1997, Kluender et al. 1998). The suitability of the stand for different end-products is tree-size dependent, since some end-products require a minimum or maximum bole size (Stevens & Barbour 2000) and stem shape also affects its suitability for some end-products. Foresters can manipulate many of the factors determining the size distribution of the trees in a stand, and it is possible, at least partially, to control the size distribution and stem shape. Therefore it should also be possible to choose a suitable stand management program that will promote desired tree characteristics (Todoroki and Carson 2003).

As outlined above, the economic outcome of forest management decisions is dependent on many uncertain factors, for example the future prices of different end-products and future harvesting costs. There is also uncertainty about the biological response to different thinning regimes. In terms of volume growth per unit area, stands' responses to thinning are relatively well known (Eriksson & Karlsson 1997), but less is known about how different thinning regimes affect the future tree size distribution and growth allocation along the stem. Knowledge of the future tree size distribution in specific stand developmental phases following different stand management programs would be of great value for economic calculations.

Objectives

The objectives of this thesis were to evaluate the extent to which the growth allocation patterns and structure of even-aged Norway spruce stands can be controlled by different silvicultural regimes. Four studies were performed to address these issues through (*i*) examining the long term influence of thinning and thinning combined with fertilisation on tree shape, (*ii*) predicting the probability of survival (not being removed for any reason) of trees in stands subjected to different thinning regimes, (*iii*) developing appropriate models for predicting the future DBH distribution of the remaining trees in different stand development stages, and (*iv*) evaluating the effect of different thinning regimes on the growth of the thickest stems.

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The data used in the studies

The data used in studies I-IV were obtained from a thinning experiment established in southern Sweden (56-63 N^o) during 1966-1980 (Figure 1). A total of 25 trials, subjected to various numbers of thinning regimes, were established at the time of the first thinning in pure even-aged Norway spruce stands. The stands were located on fertile sites, the mean SI was 32.6 and ranged between 26.9 and 40.6.

The experimental design can be considered as an incomplete block design with trials as blocks and thinnings as treatments. Some treatments were missing in some of the blocks due to difficulties in finding suitable stands large enough to include all treatments or, in a few cases, to damage caused by snow and wind.

The treatments applied were:
A. Recurrent heavy thinnings from below: 20-25 % of BA was removed at first thinning, and in subsequent thinnings all except 1-2 % of the increase in BA was removed. The number of planned thinnings was 4-6.
B. Recurrent, extra heavy thinning from below: 40-43 % of BA was removed at first thinning, and in subsequent thinnings BA was removed to the extent that the mean standing BA over time was the same as for treatment A. Treatment B was thinned every second time compared to treatment A.
C. Single, extra heavy, thinning from below, in which 63-70 % of BA was removed.
D. Recurrent, extra heavy thinning from below: 40-50 % of BA was removed at first thinning, and in subsequent thinnings all except 1-2 % of the increase in BA was removed. The number of planned thinnings was 4-6.
E. Recurrent heavy thinnings from below: the first thinning was delayed and carried out at the time of the second thinning in treatment A. Subsequent thinnings were co-ordinated in time with those in treatment A and BA after thinning was equal to that of treatment A.
F. Recurrent heavy thinnings from above: 20-28 % of the BA was removed at the first thinning. The number of thinnings and BA after thinning were equal to those of treatment A.
G. Recurrent heavy thinnings from below, combined with N-fertilisation: 20-25 % of BA was removed at first thinning, and in subsequent thinnings all except 1-2 % of the increase in BA was removed. The number of thinnings and BA after thinning were equal to those of treatment A. The first fertilisation was performed two years after the first thinning, and subsequent fertilisations were applied every fifth year.
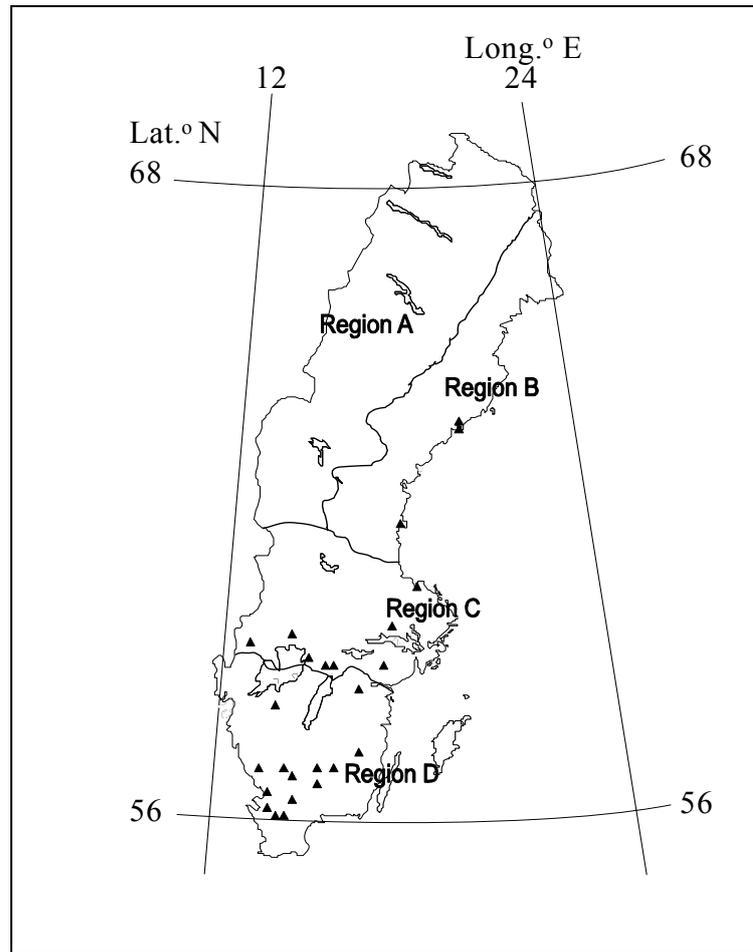**0.** Unthinned (self-thinned) control treatment.

Figure 1. Location of Norway spruce blocks (▲) in the thinning and fertilisation experiments.

Each treatment plot had an area of 0.1 ha and was surrounded by a border 10 m wide, which was treated in the same way as the plot. Every tree in each plot was permanently numbered, and its breast height level (1.3 m above ground) was permanently marked to ensure that DBH was measured at the same height on every occasion. At each assessment every tree was callipered to measure its DBH in the same two perpendicular directions (DBH_1 and DBH_2) on each occasion, and the measurements recorded were rounded to the nearest mm. The DBH used in the calculations was then found from $(DBH_1 \times DBH_2)^{0.5}$. At each assessment sample trees were selected on the plots (Karlsson 1998). Besides the DBH, the tree height above ground (H) and the height above ground of the first living branch of the sample trees were measured. Furthermore, for treatments A, C, G and 0 the bole diameter at 6 m above ground (D_{60}) was measured and used in the tree shape study (Paper I). A total of 143 plots were available and the number of study plots varied for different treatments and periods. As the stands were unaffected by N-

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fertilisation in terms of stem volume growth per unit area (Eriksson & Karlsson 1997), treatment G was excluded from the studies reported in Papers II-IV.

The thinning programme started when the dominant trees had reached a height of 12-18 m. In recurrently thinned treatments the next thinning was performed after the dominant height had increased by 3.0 m. In following thinnings the increase in dominant height between consecutive thinnings was successively reduced, ultimately to 2.0 m. The thinning and assessment intervals ranged from 4-10 years. The observation time ranged from 10 to 34 years. The number of available assessments on study plots varied for different treatments and periods (Table 1, Paper II).

Methods

Paper I

The examination of the long-term influence of thinning and thinning combined with fertilisation on the stem shape was based on two measures. The average taper in the stem section 1.3-6.0 m above ground (TAP_{60}) was used to reflect stem form, and the DBH/H ratio was used as an estimate of average taper. As trees of different sizes were suspected to be differently affected by the thinning and fertilisation treatments, the sample trees were divided into two groups - short and tall trees - with equal numbers and the two groups were analysed separately. As D_{60} was only measured for sample tree stems in treatments A, C, G and 0 the stem shape study was restricted to these treatments. The analyses were carried out using the GLM procedure in the SAS statistical package. The Tukey test was used for making multiple comparisons (SAS Institute, Inc. 1999). Treatment effects were considered significant if $p<0.05$.

Paper II

Logistic functions have been used in several studies to predict mortality (or survival) in thinned and unthinned stands (e.g. Hamilton and Edwards 1976, Hamilton 1986, Avila and Burkhart 1992, Monserud and Sterba 1999). Logistic functions should also be suitable for predicting the probability that an individual tree of a given size in a given stand will not be removed in a given thinning programme. Adequate explanatory variables can be based on the accumulated thinning intensity (ATI), the accumulated thinning quotient (ATQ), stand age at the start of the prognosis, the length of the prognosis in years, the number of active thinnings, DBH, quadratic mean DBH, basal area ha^{-1}, number of stems ha^{-1} and site index (Paper II). The site index (SI) is defined according to site curves (Hägglund and Lundmark 1982) as the mean height in metres of the 100 largest trees ha^{-1} by DBH at a stand age of 100 years. Denoting the number of assessments by t, ATI (the accumulated form of TI up to assessment t) was defined as:

$$ATI_t = \sum_{k=1}^{t} TI_k$$

and the ATQ (the accumulated form of TQ up to assessment t) was defined as:

$$ATQ_t = \frac{1}{ATI_t} \sum_{k=1}^{t} TI_k \cdot TQ_k$$

Logistic functions, tailored to the thinning methods *(i)* thinning from below, *(ii)* thinning from above and *(iii)* self-thinning were developed to estimate the probability that an individual tree will remain at specific future points in time. Application of the functions requires knowledge of the initial DBH, stand and site characteristics, number of thinnings, the length of the prediction period (number of growing seasons) and a defined thinning programme. The SAS logistic procedure (SAS Institute, Inc. 1999) was applied to the data. The tree status (coded in SAS as 0 = not removed, 1 = removed) was used as the response variable. The general formula of the logistic model is:

$p_i = 1/(1+\exp(-x_i' b))$

where p_i is the probability of not being removed for tree i, $x_i = [1\ x_{i1}\ x_{i2\ldots}\ x_{ik}]$' are the explanatory variables and $b = [b_0\ b_{1\ldots}\ b_k]$' are the parameters.

Paper III

Predictions of the future expected DBH distribution of the remaining trees at different stand development stages were generated by a series of data processing steps. Initially, the plot-wise and period-wise mean yearly DBH increments, accounting for the variations in the length of the growth period, were estimated using the initial DBH measurements and the DBH measurements obtained at later assessments. In the data set used, the information collected for each tree at each assessment was treated as a single observation, including records for the following variables: plot identity, assessment no., treatment code, tree identity and DBH. The initial data set was split, prior to analysis, and arranged in five sub-sets in which data from the first and one later assessment were included (i.e. assessment nos.1 and 2, 1 and 3, 1 and 4, 1 and 5, and 1 and 6). A bivariate model was used to estimate the fixed-effect parameters of the mean model and the parameters of the covariance model. The model used was DBH=L where L is the number of growing seasons from the first to a specific later assessment. The analyses were carried out using the MIXED procedure in the SAS statistical package (SAS Institute, Inc. 1999). The intercept calculated by SAS was used as the estimate of the initial expected DBH (μ_x) and the parameter estimate for L yielded the plot-wise and period-wise mean yearly increment (i_{obs}). The procedure also yielded an estimate of the covariance matrix.

The future DBHs of a remaining tree was estimated by

$$\hat{y} = \mu_x + iL + \frac{\rho \sigma_y}{\sigma_x}(x - \mu_x),$$

where μ_x is the initial expected DBH, x is the initial DBH of the subject tree, i is the annual expected DBH increment in mm, L is the length of the prediction period (number of growing seasons), ρ is the correlation between DBH at the initial and future stages, and, finally, σ_x and σ_y are the standard deviations of DBH at the initial and future times, respectively. Estimates of μ_x and σ_x were found from the mean and the standard deviation, respectively, of the initial DBHs whereas i, ρ, and σ_y had to be modelled in terms of characteristics of the sites, stands and thinning regimes. The mean tree part of the model can be displayed graphically (Figure 2).
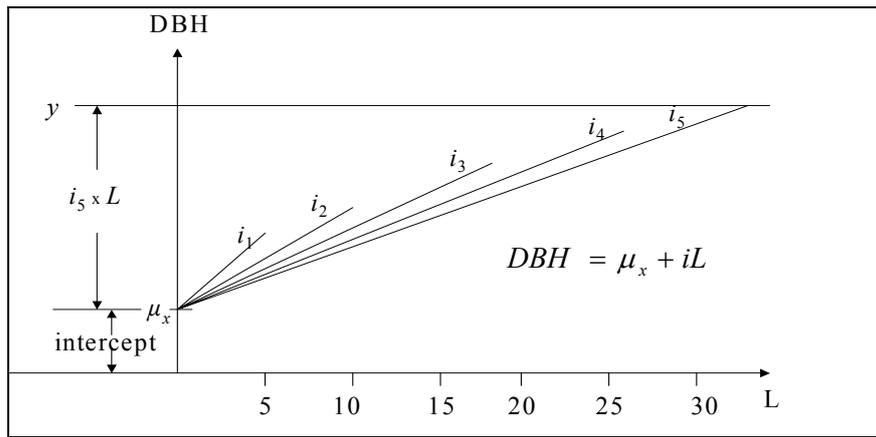

Figure 2. The principle of the mean tree modelling.

When modelling i, ρ, and σ_y the general linear regression model was used and the data were arranged so that a growth period for a plot formed an observation. A growth period was the number of growing seasons from the first and to one later assessment (i.e. assessment nos. 1-2, 1-3, 1-4, 1-5, and 1-6). Site and stand variables, expressions for the thinning strategy applied and the estimated standard deviation for the DBH of the trees in the stand at first assessment, were used as explanatory variables. The observed correlation and the estimated standard deviation for the DBH of the trees in the stand at first assessment estimates were obtained from the covariance matrix elements estimated by the MIXED procedure in SAS. The procedure REG in the SAS statistical package (SAS Institute, Inc. 1999) was used to estimate the parameters. Separate functions for the treatment groups thinning from below, thinning from above and self-thinning were applied.

Paper IV

In the study described in Paper IV the impact of thinning on the growth of the largest stems by DBH ha^{-1} was analysed. The actual DBH increase (AI) and the genuine DBH increase (GI) was defined for D100, D200, D300 and D400 (i.e. mean DBH of the 100, 200, 300, and 400 largest stems by DBH ha^{-1}). For a given DBH fraction the AI for a stand was defined as the difference between the mean DBH of the actual DBH fraction stems at two points in time. The GI is defined

similarly to AI, but only those stems that qualified for inclusion in the fraction of largest stems by DBH at the latest assessment were accounted for in the calculations of the mean DBH at earlier stages. The increases in AI and GI in each of five growth periods following the first thinning for six different thinning regimes were compared by analyses of variance to the corresponding values in unthinned stands. The procedure GLM in the SAS statistical package (SAS Institute, Inc. 1999) was used in the analyses and, due to the unbalanced design, least square means were used as indicators of the typical response for each treatment group. The model applied was:

$y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$

where y_{ij} is the observed yield for treatment i, block j; μ is the overall mean; α_i is the effect of treatment i; β_j is the effect of block j and ε_{ij} is the random error. Pairwise one-sided comparison significance tests (overall $p = 0.05$) were performed, in which Dunnett's method was used to compare the thinned treatment means to the control treatment mean. In addition, the difference between AI and GI was calculated and the expected D100, D200, D300 and D400 at future points in time were modelled using mixed linear regression. Explanatory variables, obtained at the time for the first thinning, were found from variables describing the thinning regime and variables characterising the sites and stands.

Results

Paper I

Thinnings affected the growth allocation pattern, causing more growth to be allocated to lower parts of the stem. After an extra heavy thinning at the first assessment (TI about 0.7), the remaining stems responded markedly to the thinning and within six years the TAP_{60} had increased 2 mm m^{-1} compared to the taper in the unthinned stands. After 25 years the difference in TAP_{60} to the unthinned control had increased to 3.5 mm m^{-1}. Recurrently heavy thinned stands also showed increases in TAP_{60} compared to unthinned stands, but the differences were statistically significant only for short stems. No effect of N-fertilisation on TAP_{60} was detected in recurrently thinned stands. The differences detected in the TAP_{60} were equivalent to the corresponding D/H differences. Tall trees became more conical compared with short trees in the same stand, but the differences between treatments were equal, regardless of the tree size.

Paper II

The probability graphs yielded by the functions based on mean values of the independent variables for the different treatments at assessments 1-6 were used in the verification of the functions. The probability graphs for survival, for stands thinned from below and self-thinned stands both had a clear S-shape, i.e. smaller trees were more likely to be removed, while the probability graph for survival was bell-shaped for stands thinned from above. The functions produce probability curves for different treatments and over time that appear to be consistent with

expectations. For example, the function for thinning from above strongly decreases the probability for larger trees to remain and increases the probability for smaller trees to remain compared to trees in unthinned stands and in stands thinned from below. Also, thinning according to treatment C (heavily thinned at the first assessment and not thinned subsequently) shows a slight decrease in the remaining probability over time, mirroring some irregular mortality. Furthermore, trees in stands that were most heavily thinned overall (treatment D), exhibited the lowest probability to remain at later assessments (Figure 3).
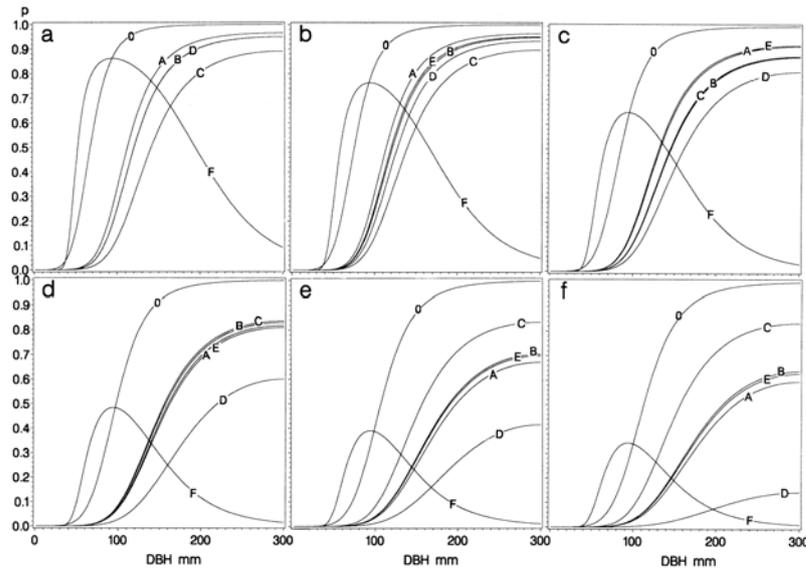

Figure 3 *a-f.* Probability (*p*) curves generated by the functions for thinning from below (treatments A-E), thinning from above (treatment F) and self-thinning (treatment 0) using mean values of the explanatory variables for the different treatments at assessments 1-6. The curves for each treatment are marked with the corresponding treatment codes. Panel *a* shows the outcome at the time for assessment 1, panel *b* at assessment 2 and so on. (In panel *a,* the curves for treatment B and D coincide and the curve for treatment E – not yet thinned – has been excluded).

Paper III

The fit of the models predicting the DBH distribution of the trees remaining after different thinning regimes was validated by examining the means and standard deviations of the differences between observed and predicted future DBHs for different lengths of periods and treatments. The mean difference varied from -3.1 to 4.6 mm depending on the length of the prediction period (21, 27 and 33 years) and treatment groups (A-E, F and 0). As expected, the standard deviation increased as the prediction period increased. For unthinned stands (treatment 0) the standard deviations were 21, 25 and 33 mm after 21, 27 and 33 years, respectively. The corresponding values for stands thinned from below (treatments

A-E) were 30, 34 and 40 mm, and for stands thinned from above 26, 30 and 43 mm (Table 4, Paper III). When observed DBHs were plotted against predicted DBHs no serious anomalies were detected, but the DBH of small diameter trees was generally overestimated (Paper III, Figure 1).

Paper IV

The AI and GI increases in DBH observed for thinned treatments in five growth periods for D100, D200, D300 and D400 were compared through analyses of variance to the corresponding figures in the unthinned treatment. In order to simplify the comparisons the original lengths of the periods were all transformed to a 7-year period.

The analyses for AI showed that heavily thinned treatments (B, C, and D) at assessment 1, already after one period displayed significantly larger mean DBH increase for all studied fractions compared to the unthinned treatment. In later stages, the thinning affected the mean DBH significantly for all treatments, except treatment F (thinning from above). For the treatments A-E, 35 years after the first thinning, the DBH fraction means for thinned treatments had increased 2.6-9.0 cm more than the corresponding values in unthinned stands (Table 3, Paper IV).

For periods 1 and 2, treatment C (heavily thinned at the start of the experiment; TI about 0.7) showed the highest GI, but the GI associated with treatment C subsequently declined in subsequent periods. After 35 years, the GI for D100, D200, D300 and D400 for thinned stands had increased 5 – 11 cm more than the corresponding values in unthinned stands, and the increase in GI was most pronounced in the extra heavily thinned treatment D (Table 4, Paper IV).

Thinning of larger trees decreases the AI for the D100, D200, D300 and D400 stems. Consequently, the difference between GI and AI for treatment F was three times as high as the corresponding difference for treatment A. Treatment F is thinned from above and treatment A thinned from below, but the overall ATI of the two treatments is the same. The unthinned treatment showed the smallest difference between GI and AI, due to the minimal effect of selection (Table 7, Paper IV).

The functions predicting the future D100, D200, D300 and D400 seem to yield good estimates of future DBH fraction means within the range of the variations of stand treatments included in the study.

Discussion

This thesis deals with the impact of different silvicultural regimes on stem shape and growth of the diameter at breast height (DBH), based on data from permanent sample plots included in a region-wide experiment in which various thinning and fertilisation treatments were applied to even aged Norway spruce stands. The expected DBH growth after different thinning regimes was addressed by forming empirical growth models tailored to the thinning methods *(i)* thinning from below, *(ii)* thinning from above and *(iii)* self-thinning. The growth models consist of (*i*) a sub-model predicting which tree will remain after conducting a defined thinning programme and (*ii*) an associated model estimating the DBH growth of the remaining trees. In a complementary study the thinning effect on the DBH growth of the largest stems by DBH ha^{-1} was addressed.

The development of stem shape following different stand management regimes

Many researchers have confirmed the general theory that thinnings tend to shift the allocation of growth downward along the stem (Gray 1956, Larson 1963, Myers 1963, Borosowski & Kolosowski 1971). In a study regarding form and taper in lodgepole pine *(Pinus contorta var. latifolia* Engelm.) Muhairwe (1994) concluded that changes in these variables were closely related to crown size, which, in turn, is related to stand density. As trees grow the level of competition among them increases. This causes the live crown to recede through self-pruning, and in response assimilates tend to be allocated higher up in the stem. Thinnings decrease stand density, thereby reducing the intensity of competition. Consequently, self-pruning would be expected to decrease or stop, and the proportion of assimilates allocated to lower parts of the stem should increase.

The results of the investigations this thesis is based upon support the general theory. For trees in stands subjected to extra heavy single thinnings the growth was shifted markedly downwards along the stem. Trees in stands subjected to recurrent heavy thinnings responded in similar ways, but differences in stem form and taper between these trees and those in unthinned stands were not always statistically significant.

Results from studies concerning the effect of N-fertilisation on tree shape are conflicting. Snowdon et al. (1981) and Valinger (1992) reported that growth was allocated upwards along the stem after fertilisation, whereas Sterba (1978), Gordon & Graham (1986) and Mead & Tamm (1988) found the opposite. Miller & Cooper (1973), Groot et al. (1984), Thomson & Barclay (1984) and Wiklund et al. (1995) found that N-fertilisation had no effect on stem form. Thomson & Barclay (1984) and Valinger (1992) reported that the combination of thinning and N-fertilisation had no effect on stem form. In the study reported in Paper I, the stem form and taper of trees in thinned Norway spruce stands were found to be unaffected by the combined treatment of thinning and N-fertilisation (treatment G)

compared to equally thinned but not fertilised stands (treatment A). This is consistent with results from a study by Eriksson & Karlsson (1997) based on the same experimental material, who found no differences in stem volume growth per unit area between treatments A and G.

The length and distribution of the live crown along the stem can be manipulated by regulating stand density. In this way foresters can partially control the stem shape, and thus indirectly affect timber quality variables related to stem taper, especially those of the first log. In the study reported in Paper I short trees had lower TAP_{60} and D/H values compared with tall trees. This consistent with known relationships between stem shape and crown development. For all treatments, the crown ratio (length of live crown divided by tree height) was lower for short trees than for tall trees (Table 3, Paper I).

Predicting which individual trees will remain after different thinning regimes

It was hypothesised that the probability that a tree will remain in a stand at different stand development stages could be modelled using (*i*) appropriate summary measures reflecting the intended thinning strategy over time and (*ii*) certain characteristics about the stand and site recorded at the time for the first thinning. As logistic functions have been widely used to predict the probability that a tree in a stand will be removed by natural mortality (Avila & Burkhart 1992, Hamilton 1986, Monserud & Sterba 1999, Yang et al. 2003), logistic functions should also be useful for predicting the probability that a tree will remain in a stand subjected to active thinnings. However, no earlier studies addressing this possibility were found.

In a first step towards developing such functions, attempts were made in the studies this thesis is based upon to fit a common function for all of the thinning strategies applied. However it was not possible to find a common function with a satisfactory fit, at least with the available set of explanatory variables, since the curves generated by plotting the probability that trees would remain against DBH were S-shaped for stands thinned from below and self-thinned stands, while the corresponding curves for stands thinned from above were bell-shaped. Therefore, the data-set was first split into two parts consisting of (*i*) data related to stands thinned from below and unthinned stands and (*ii*) data related to stands thinned from above. Secondly, as an improved fit was obtained after further splitting the data related to stands thinned from below and unthinned stands, the fitting procedure ended up with three functions tailored for (*i*) stands thinned from below, (*ii*) stands thinned from above and (*iii*) self-thinned stands. After the initial modelling it was apparent that further factors had to be considered to obtain a satisfactory common model for different thinnings from below. The main problem was connected to treatment C (thinned once, extra heavily). To obtain a satisfactory common model for stands thinned from below a set of weight variables had to be included in the model (Paper II).

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Data on a Norway spruce thinning experiment situated in south-eastern Sweden (Johansson & Karlsson 2004) studied over a 39-year period with treatments similar to the treatments A (A-2), B (B-2), C (C-2) and 0 (0-2) in the study described in Paper II were available for an independent test of the functions
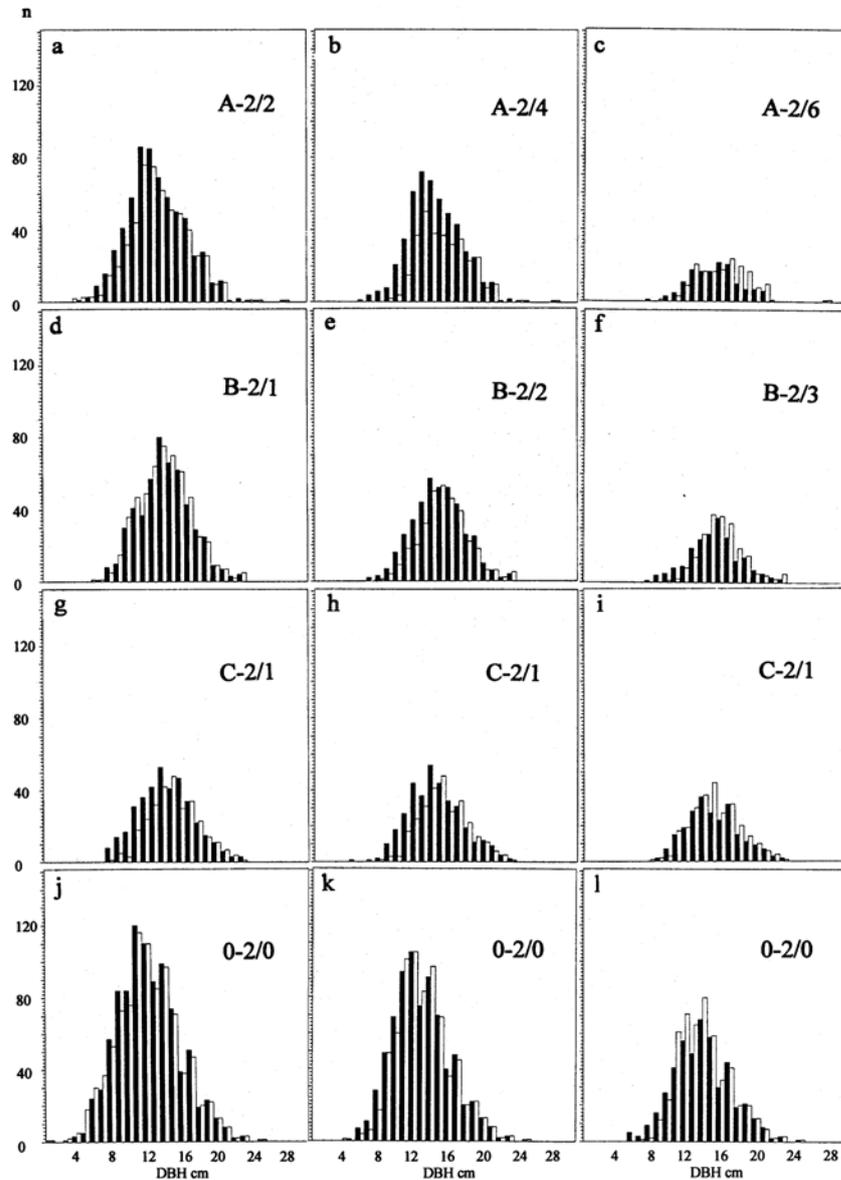

Figure 4 *a-l.* Results of applying the functions presented in Paper II estimating which trees will remain after different thinning strategies, to an independent experiment, showing the predicted (black bars) and observed (white bars) numbers of remaining trees (n) at assessments 2 *(a, d, g, j)*, 4 *(b, e, h, k)* and 6 *(c, f, i, l)* DBH in 1 cm classes. The treatment codes/numbers of active thinnings are shown in the graphs.

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predicting which trees will remain in stands thinned from below and unthinned stands. Predicted vs. observed numbers of stems in 1 cm DBH classes for the treatments represented at assessments 2, 4 and 6 (i.e. after 5, 17 and 34 years) are shown in Figure 4. The treatment similar to treatment A in the study reported in Paper II involved thinning at assessments 1 - 6, the treatment similar to treatment B involved thinning at assessments 1, 3 and 5 and the treatment similar to treatment C involved thinning at assessment 1. The most striking observation from the data shown in Figure 4 is that the predicted remaining number of stems in small DBH-classes after two and four thinnings according to treatments A and C were overestimated (Figure 4a, 4b, 4g and 4h).

Comparison of the predicted and observed numbers of stems in 1 cm DBH classes, based on the Hosmer-Lemeshow goodness-of-fit test (Hosmer & Lemeshow 1989) and published graphs (Figure 2 in Paper II and Figure 4), indicates that knowledge of the DBH distribution and characteristics of the stand and site at the time for the first thinning provides sufficient information to obtain reasonable predictions about which individual trees will remain after a defined thinning programme.

The probability predictions obtained from the functions are based on information available at the time for the first thinning and a designed thinning program. Consequently, sets of trees that are likely to remain at different stand development stages could be predicted by adapting the explanatory variables to the intended stages. A computer program would be needed for convenient calculations. As the logistic functions simply yield probabilities that trees of certain sizes will not be removed, decisions regarding whether specific trees will be removed or not can easily be performed by a computer's random number generator.

Expected DBH distributions after different thinning regimes

A DBH distribution may be characterised by its location and variability. A more detailed characterization may also consider its skewness and kurtosis. Skewness is a measure of symmetry, or more precisely, the lack of symmetry. If a variable is normally distributed its skewness and kurtosis are zero. If the skewness is greater than zero, the distribution is skewed to the right, and there are more observations to the left than to the right of the mean. Kurtosis is a measure of whether the data are peaked or flat relative to a normal distribution (Sharma 1996). That is, data sets with high kurtosis tend to have a distinct peak near the mean and decline rather rapidly. Data sets with low kurtosis tend to have a flat top near the mean rather than a sharp peak. If the kurtosis is less than zero the distribution has thicker tails than a normal distribution. From the data set used in studies III and IV, plot-wise mean values of the observed measures of the location (the arithmetic DBH mean), variability (standard deviation of DBH), skewness and kurtosis, for each treatment and assessment are shown in Table 1.

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The differences between treatments in the arithmetic mean DBH shown in Table 1 are consequences of the combined effects of increased DBH growth due to thinning and, in practically all cases, the fact that the removed trees are not evenly distributed across the diameter range, due to selection. The data in Table 1 show that heavily thinned treatments result in larger arithmetic DBH means. When modelling the diameter increment for thinning from below, the parameter estimates for ATI, ATQ, the mean distance between the stems in the initial stand and site productivity all had positive signs. Consequently, diameter growth is promoted by high levels of these factors (Paper III). For example, at assessment six, on average 33 years after the first thinning, the mean DBH for the most heavily thinned treatment (D), is twice as high as for treatments F and 0 (thinning from above and no thinning, respectively).

Theoretically, it should be possible to make a DBH distribution gradually tighter than it was at the time for the first thinning by applying a series of thinnings, preferably from below. However, this expectation is not supported by the data (Table 1). Thinnings from below seem only to slow the increase in standard deviations over time compared to thinning from above and leaving stands unthinned. The data in Table 1 show that the standard deviation of DBH increases over time for all treatments and, consequently, the parameter estimates for the explanatory variable "number of growing seasons" had a positive sign in the function estimating future expected DBH variance (Paper III). At the end of the studied period, treatment F (thinning from above) shows the most extended distribution followed by treatments 0 (no thinning) and C (a single heavy thinning). An overall illustration of the impact of different thinning strategies on the expected DBH distribution is shown in Paper III (Figure 1).

All thinning regimes tend to increase the DBH growth of individual stems compared to the stems in unthinned stands and the increased DBH growth is highly affected by the accumulated thinning intensity. If the aim is to produce stems with a large DBH within a given length of the rotation period, thinnings according to treatment D should be carried out. Almost all remaining trees in stands subjected to the D-thinning regime had DBHs between 25 and 50 cm 30-34 years after the first thinning (Paper III, Figure 1). Thinnings according to treatment C allow very initially rapid DBH growth, but in later stages, following increases in tree sizes and thus in competition between neighbouring trees, the DBH growth declines. The DBH distribution at the time for the final cutting in stands subjected to treatment C depends to a large extent on the number of stems remaining after the extra heavy single thinning and the survival of these stems. Compared to corresponding growth in unthinned stands, only the C-thinning regime causes a marked reduction in volume growth per unit area. The reduction is about 20 percent in early stages after the (first) thinning and 10 percent in later stages (Eriksson & Karlsson 1997).

The mean DBH of the remaining trees in unthinned stands did not deviate from the corresponding values in stands thinned from above (Table 1). However, compared to unthinned stands, a flatter top near the mean was observed for stands

thinned from above. This observation was supported by lower kurtosis values for stands thinned from above (Table 1).

With the exceptions of low kurtosis for stands thinned from above (treatment F), especially at assessments 4 and 5, the measures of skewness and kurtosis did not reveal any clear treatment-dependent pattern (Table 1). This observation may be associated with a persistent problem of classical DBH distribution modelling by

Table 1. Observed mean values associated with the DBH distributions used in studies II - IV. Measures of the DBH location (the arithmetic DBH mean), DBH variability (standard deviation of the DBH), skewness and kurtosis for different treatments before any thinnings at assessments 1-6 are shown. The number of observations can be extracted from Table 1 in Paper II.

		Treatment code						
		A	B	C	D	E	F	0
Assessment 1	DBH (mm)	116	113	112	109	119	111	114
	Std. dev.	34.2	36.5	35.4	37.3	35.0	35.2	35.3
	Skewness	0.00	0.05	0.03	0.22	0.13	0.19	0.09
	Kurtosis	0.08	0.10	0.18	-0.24	-0.08	-0.16	0.25
Assessment 2	DBH (mm)	154	167	201	168	146	131	136
	Std. dev.	33.6	34.2	32.0	34.6	36.4	38.2	39.0
	Skewness	0.17	0.24	0.05	0.10	0.31	0.14	0.16
	Kurtosis	-0.08	-0.14	0.17	-0.13	-0.07	-0.32	-0.22
Assessment 3	DBH (mm)	190	194	243	218	190	153	155
	Std. dev.	36.4	40.3	39.2	38.1	39.6	44.5	43.7
	Skewness	0.14	0.21	0.05	0.10	0.30	0.09	0.20
	Kurtosis	0.03	-0.20	0.04	0.20	-0.14	-0.28	-0.20
Assessment 4	DBH (mm)	237	252	279	278	236	177	177
	Std. dev.	40.6	41.9	46.4	39.2	43.5	51.6	48.2
	Skewness	0.20	0.18	0.00	0.21	0.29	0.11	0.27
	Kurtosis	0.12	0.36	0.02	0.28	-0.09	-0.44	-0.14
Assessment 5	DBH (mm)	271	279	305	342	271	194	195
	Std. dev.	45.2	48.6	53.9	45.8	47.5	68.4	53.7
	Skewness	0.36	0.02	-0.14	0.40	0.10	0.16	0.41
	Kurtosis	0.68	-0.16	-0.26	0.61	-0.16	-0.73	-0.01
Assessment 6	DBH (mm)	284	334	312	396	282	194	203
	Std. dev.	47.3	49.8	57.8	42.6	52.3	65.5	54.4
	Skewness	0.42	0.10	-0.04	0.04	0.25	0.28	0.43
	Kurtosis	0.80	-0.60	-0.39	0.61	0.27	-0.58	-0.18

means of probability density functions; the difficulties involved in identifying biologically meaningful relationships between measurable stand characteristics and the shape parameters of the DBH distribution (Knobel & Burkhart 1991).

As the arithmetic mean DBH may be influenced by large numbers of small DBH trees, the mean DBH of some fraction of the largest stems by DBH ha^{-1} would be a helpful summary measure when assessing the suitability of the main crop trees (especially) in the final stand for specific end-products. Also, larger DBH trees account for a proportionately greater share of a stand's profitability. In the study described in Paper IV, the D100, D200, D300 and D400 for six different thinning regimes were compared to the corresponding stems in unthinned stands. The thinning strategy applied had a major impact on the DBH distribution of the stems in the residual stand. By adopting a thinning strategy with a high ATI the D100, D200, D300 and D400 can be increased by up to 9 cm after 35 years, compared to the corresponding values in unthinned stands.

Data from the previously mentioned Norway spruce thinning experiment situated in south-eastern Sweden studied over a 39-year period with A-2, B-2, C-2 and 0-2 treatments (Johansson & Karlsson 2004) were used for an independent test of the functions predicting the future DBHs. Predicted and observed future DBHs for treatments represented at assessments 3, 5 and 7 (i.e. after 10, 24 and 39 years) are shown in Figure 5. The A-2-treatment was thinned at assessments 1 - 6, the B-2-treatment at assessments 1, 3 and 5 and the C-2-treatment at assessment 1. The overall picture is that the functions produce reasonable estimates, but the DBH of thick stems is underestimated, especially in later stages, and the DBH of thin stems is overestimated in earlier stages for treatment C-2 (Figure 5). The prediction time of 39 years is somewhat outside the scope of the functions.

Actual and genuine DBH increases following thinning

The differences between genuine and actual increases (GI and AI, respectively) are due to some stems being removed and some being replaced as a result of differences in the DBH growth between individual trees in each growth period considered. The biological response to thinning of different fractions of the largest stems by DBH may be defined as the difference between GI for thinned stands and GI for unthinned controls, according to Table 4, Paper IV. The AI fractions of the largest stems by DBH in the residual stand would be of most interest from a practical view. However, since GI reflects the growth of the same trees over time GI would be a more suitable measure than AI for studying the effects of biological responses to thinning on the DBH growth. The AI over time for different fractions of the largest trees by DBH for the unthinned control stands and stands thinned from above did not significantly deviate (Table 3, Paper IV). This implies that all the DBH increases due to the biological response to thinning for treatment F, about 5 cm over 35 years, were successively harvested in the thinnings. Treatment B (thinned at the beginning of periods 1, 3 and 5, i.e. every second time compared to treatment A, but with the same ATI overall) displayed larger GI values than treatment A. This observation indicates that fewer thinnings may promote the

DBH growth of the largest trees when the thinning intensity over time is of equal strength. Treatment D (most heavily thinned) displayed the most pronounced GI; about 10 cm larger after 35 years for D100 and D200, compared to the unthinned control. Treatment C (heavily thinned at the start of the experiment; ATI about
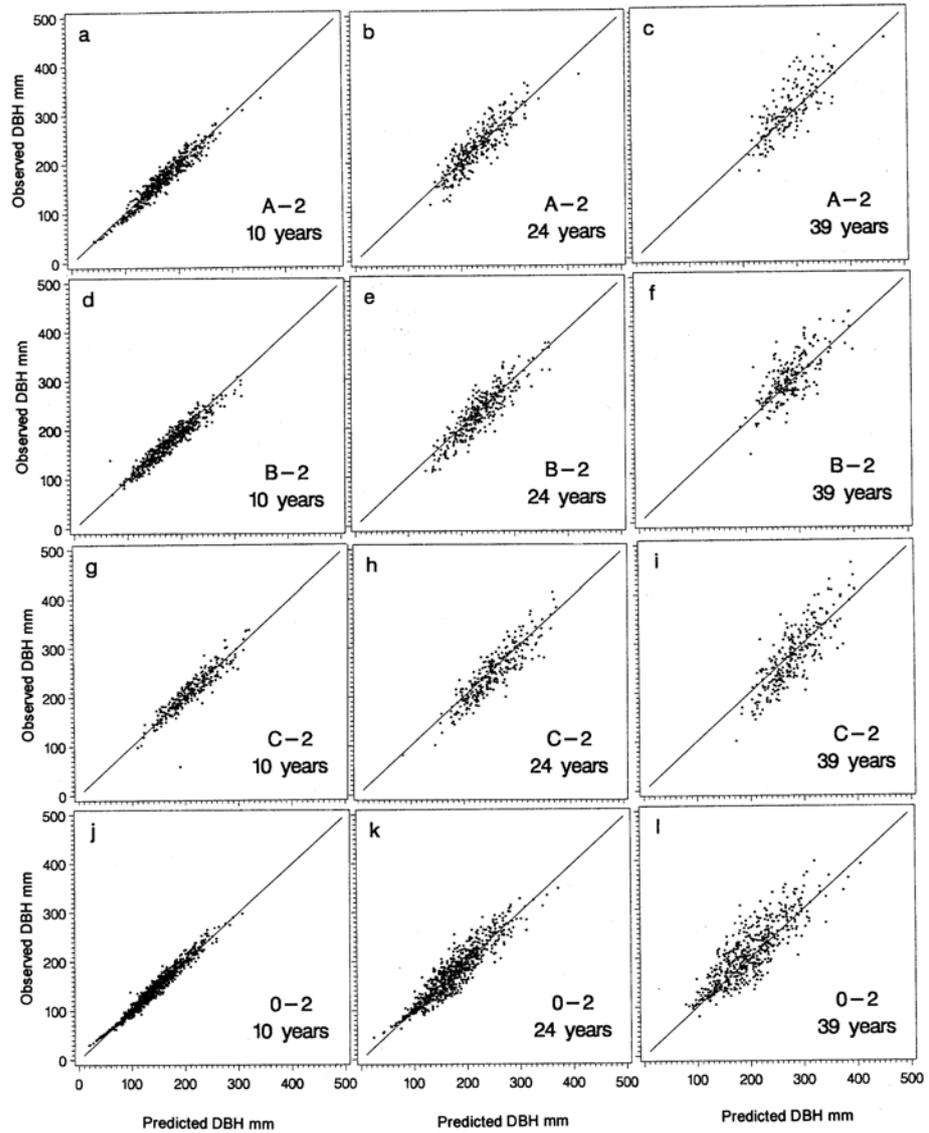

Figure 5. Results of applying the functions presented in Paper III for estimating future DBHs after different thinning strategies to data from an independent experiment, showing predicted and observed future DBHs for treatments represented at assessments 3, 5 and 7. The treatment codes and the lengths of the prediction period (years) are shown in the graphs. In each case the diagonal line is the line of equivalence.

0.7), showed the highest GI for periods 1 and 2, but in later periods the GI declined. The thinning method does not seem to affect the GI. Treatments A (thinning from below) and F (thinning from above) with equal ATI, both yielded about 5 cm larger GI after 35 years compared to the control for all the DBH fractions studied. The biological response to thinnings for treatments A, E and F were all about 5 cm over 35 years, indicating that the ATI, but not the ATQ, has an impact on the DBH response to thinning. (Table 4, Paper IV). When interpreting the results, attention should be paid to the fact that more growth substances are needed to obtain a given DBH increment for thick stems than for thin stems.

DBHs at harvesting time

One way to compare the DBH growth after different thinning regimes is to compare the DBHs attained at the time for removal. The outcome in this respect was investigated at selected localities included in the Norway spruce experiment used in studies II-IV. The criteria used for selecting localities for this analysis were that observations had to be available from a long period (at least 30 years) from the first thinning and all of the treatments (A-F and 0) had to have been applied to the stands. A total of four localities met these criteria. Trees that had been removed (by regular mortality, irregular mortality and active thinning) at any assessment and the remaining trees at the last assessment were distributed into five DBH classes, *(i)* all trees (≥ 0 cm), and trees with a DBH greater than *(ii)* 10 cm (≥ 10 cm), *(iii)* 20 cm (≥ 20 cm), *(iv)* 30 cm (≥ 30 cm) and *(v)* 40 cm (≥ 40 cm). The subplot figures were transformed to per hectare figures for the analysis (Table 2).

Table 2. Number of stems ha^{-1} with DBHs $\geq$ 0, 10, 20, 30 and 40 cm at removal time in stands subjected to different thinning regimes. (The corresponding percentages of total stems are shown in parenthesis)

DBH	Thinning regime (treatment) code
	A	B	C	D	E	F	0
≥ 0 cm	3565	3269	3556	3157	3210	3503	3583
	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)	(100.0)
≥ 10 cm	1995	1891	1694	1761	2062	2145	2218
	(56.0)	(57.8)	(47.6)	(56.1)	(64.2)	(61.2)	(61.9)
≥ 20 cm	765	706	617	646	766	797	867
	(21.4)	(21.6)	(17.4)	(20.1)	(23.9)	(22.8)	(24.2)
≥ 30 cm	229	326	297	283	247	135	190
	(6.4)	(10.0)	(8.4)	(9.0)	(7.7)	(3.9)	(5.3)
≥ 40 cm	17	47	42	78	20	7	10
	(0.5)	(1.4)	(1.2)	(2.5)	(0.6)	(0.2)	(0.3)

The figures in Table 2 indicate that *(i)* if the aim is to produce many large DBH stems (≥ 30 cm) within a given rotation period, thinnings from below (treatments A-E) should be carried out, *(ii)* extra heavy thinnings from below (treatment D) promote the growth of extra large (≥ 40 cm) DBH stems, and *(iii)* if stems with a

DBH ≥ 20 cm are satisfactory, thinning from above and no thinnings may be acceptable strategies.

Interactions between stem form changes, DBH growth and stem volume growth per unit area

Stand density affects the form and taper of stems. As trees grow the level of competition amongst them increases. This causes the live crown to recede through self-pruning, and in response, assimilates tend to be allocated higher up in the stem. Thinnings decrease stand density and reduce the competition intensity, stop or reduce self-pruning, and increase the relative allocation of assimilates to lower parts of the stem. By regulating the stand density the length and distribution of the live crown along the stem can be manipulated (see, for instance, Larson 1963), and consequently trees growing in dense stands become less tapered (Paper I). On a given site with trees of a given genetic stock, the DBH growth after thinnings strongly depends on the residual stand density (Paper III). The DBH growth will be delayed if a high-density approach is chosen (Papers III and IV). Consequently, the aims to achieve rapid diameter growth and low stem tapering cannot be realised simultaneously, so the silvicultural regimes must reflect a compromise between these, and other, production objectives. For example, in treatment C (heavily thinned in a single tinning; TI about 0.7) the growth of the 100-400 largest stems ha^{-1} by DBH was on average about 7 cm larger after 35 years, compared to the corresponding trees in unthinned stands (Table 3, Paper IV). The increase in taper due to the thinning was 0.35 cm m^{-1} (Paper I), i.e. the difference in bole diameter 6 m above ground between unthinned stands and stands that were heavily thinned once was reduced to about 5.5 cm. Thinning according to treatment C causes loss of volume growth per unit area by about 10 percent after 25 years compared to that in unthinned stands (Eriksson and Karlsson 1997). A series of thinnings from below (treatment A) also led to taper being increased, but not always significantly, compared to that of trees in unthinned stands. The stem volume growth per unit area in these stands was slightly less than the volume growth in the unthinned stands, but the differences were not statistically significant (Eriksson & Karlsson 1997).

Practical implications, conclusions and further research

The economic outcome of forest management is highly dependent on the thinning regime applied, and an almost infinite number of alternative thinning regimes could be applied (Pukkala et al. 1999). A prerequisite for choosing a suitable thinning regime is knowledge about the biological response to thinning of the remaining trees in a stand. The effects of different thinning regimes on wood properties and stem quality have been investigated by Pape (1999a, b, c), and differences in stem volume growth per unit area after different thinning regimes by Eriksson & Karlsson (1997). However, the growth allocation along the stems and

the DBH growth of the individual trees in stands subjected to different thinning regimes had not been thoroughly investigated prior to the studies described in Papers I-IV. The findings reported in these papers provide knowledge about the effect of different thinning regimes on the growth allocation pattern along the stem and the expected DBH distribution of the remaining trees in a stand that can be included in considerations when choosing a thinning regime. As the outcome of different thinning regimes is dependent on the stand characteristics at the time for the first thinning the findings of studies I-IV may also affect the stand establishment routines and the pre-commercial thinnings.

The analyses of expected stem growth in stands subjected to various thinning regimes show that
- heavy thinnings increase stem form and taper
- N-fertilization has no effect on stem form and taper
- low tapering cannot be combined with rapid DBH growth
- heavy thinnings from below promote high frequencies of thick stems and extra heavy thinnings promote high frequencies of extra thick stems
- thinning from above (or no thinnngs) may be viable alternatives to thinning from below if a main crop consisting of stems with a medium DBH is a satisfactory outcome
- the actual mean DBH of thick stems compared to the corresponding figure in unthinned stands can be increased by up to 2.6 mm per year if extra heavy thinnings are carried out
- the biological response to thinning of thick stems is influenced by the thinning intensity, but not by the thinning method
- the variation in DBH increases over time but increases more for stands thinned from above and unthinned stands compared to stands thinned from below.

Given a defined thinning regime and data about the stand and site conditions at the time for the first thinning, reasonable estimates at different stages during the rotation period can be obtained for
- the probability that stems of different DBH classes will remain in the stand
- the future DBH of the remaining stems
- the future mean DBH of specific fractions of stems with the highest DBH in the stand

The functions presented in the studies described in Papers II and III provide growth models for predicting the future DBH distribution in Norway spruce stands, which have not been previously thinned, following different thinning regimes. A prerequisite for extensive use of any growth model is that the functions and routines concerned must be implemented in user-friendly computer software. In the present case, such software remains to be developed. The models could also be further developed by incorporating a tree height growth function, which combined with the DBH data would allow the stem volume of trees in the stand to be calculated.

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Acknowledgements