Growth of Genetically Improved Stands of Norway Spruce, Scots Pine and Loblolly Pine

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Abstract

Genetically improved material of Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and loblolly pine (*Pinus taeda* L.) is commonly used for forest regeneration in Sweden and the south-east of the USA. The potential genetic gain in terms of volume growth is, at present, in the range 10-20 % for Norway spruce and Scots pine and similar or even greater for loblolly pine, and will increase in the future. As a basis for optimizing management, it is necessary to have accurate growth and yield forecasts that take genetic improvement into consideration. The objective of this research was to analyze and model the effects of tree improvement on tree growth and tree slenderness (height-diameter ratio).

Results from two field trials of Scots pine and loblolly pine showed that genetics and spacing affected both tree growth and tree slenderness, indicating that growth models need to consider genetics as well as competition to predict the development of various genetic entries correctly (Paper I, II). Paper III described the development of a height growth model for unimproved material and this was subsequently evaluated for various genetic entries of Norway spruce and Scots pine. The analysis indicated that the model predicted the height development relatively well for genetically improved Norway spruce. However, for Scots pine, the model needed to be modified. By incorporating a genetic component, the prediction errors were significantly reduced for Scots pine. The phenotypic plus-tree selection conducted during the 1970s and 1980s was found to have little impact on the height-diameter ratios for Norway spruce and Scots pine in Sweden (Paper IV). Small differences in height-diameter relationships were also found for loblolly pine seedling entries in the south-eastern USA (Paper II). However, the moderate heritability of height-diameter ratio for Norway spruce and Scots pine indicates that breeding can modify such ratios (Paper IV). Selecting for diameter only would result in less slender stems of both species, while selecting for height only would result in less slender Norway spruce trees and more slender Scots pine trees.

Keywords: Norway spruce, Scots pine, loblolly pine, genetically improved material, tree improvement program, growth models, height-diameter relationship

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Sammanfattning

I mer än 60 års tid har det bedrivits traditionellt förädlingsarbete för gran (*Picea abies* (L.) Karst.) och tall (*Pinus sylvestris* L.) i Sverige och för loblollytall (*Pinus taeda* L.) i sydöstra USA. Till följd av detta arbete är de flesta skogsplantor genetiskt förädlade i dessa länder. En av fördelarna med förädlat material är att de producerar mer volym jämfört med oförädlat material. Förädlad gran och tall i Sverige beräknas producera 10-20 % mer volym, medan förädlad loblollytall beräknas producera 10-30 % mer än oförädlat material. Dessa produktionsökningar kan innebära att dagens tillväxtmodeller, som är baserade på oförädlat material, måste justeras för att korrekt kunna prognosticera framtida volymer. Syftet med denna avhandling var att studera tillväxten hos förädlat material och att infoga dessa effekter i dagens tillväxtmodeller för gran och tall.

Resultat från ett tall- och ett loblollytallförsök pekade på att både genetik och stamantal påverkar trädens tillväxt och deras stamform, vilket tyder på att tillväxtmodeller måste kunnna beakta både trädens genetik och konkurrens mellan träden för att kunna prognosticera deras utveckling på ett tillförlitligt sätt (Studie I, II). I studie III presenterades en tillväxtmodell för oförädlad ungskog av tall och gran. Denna modell visades vara tillförlitlig för förädlad gran. För tall däremot, fanns det stora prognosticeringsproblem och för att bättre kunna prognosticera förädlad tall, infogades därför en genetisk komponent i modellen. Den genetiska komponenten baserades på trädens genetiska potential och anpassades utifrån ett stort antal fältförsök. Studie IV undersökte hur 70- och 80-talets plusträdsurval av gran och tall i Sverige påverkade trädens stamform (höjd-diameter kvot). Utifrån ett stort antal fältförsök och data från andra omgångens plusträdsurval visades att förädlat material har en liknande stamform som oförädlat material. Liknande resultat presenterades även i studie II där stamformsskillnader mellan olika genetiska enheter av loblollytall i sydöstra USA undersöktes. Resultaten pekade generellt på små stamformsskillnader. Resultaten från studie IV pekade samtidigt på att stamformen är en ärftlig egenskap, vilket gör det möjligt för skogsträdsförädlingen att påverka trädens stamform. Exempelvis skulle träden bli mindre slanka om förädlingen systematiskt skulle välja träd med stor diameter.

Dedication

To my family

...essentially, all models are wrong, but some are useful

George Box

Contents

List of Publications

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

I Egbäck, S., Liziniewicz, M., Högberg, K-A., Ekö, P-M., Nilsson, U. (2012). Influence of progeny and initial stand density on growth and quality traits of 21 year old half-sib Scots pine (*Pinus sylvestris* L.). *Forest ecology and management* 286, 1-7

II Egbäck, S., Bullock, B., Isik, F., McKeand, S. (2015). Height-Diameter Relationships for Different Genetic Planting Stock of Loblolly pine at Age Six. *Forest Science 61, 424-428*

III Egbäck, S., Nilsson, U., Nyström, K., Högberg, K-A., Fahlvik, N. Modeling early height growth in trials of genetically improved Norway spruce and Scots pine in southern Sweden (manuscript)

IV Egbäck, S., Karlsson, B., Högberg, K-A., Nyström, K., Nilsson, U. Effects of phenotypic selection on the height-diameter ratio of Norway spruce and Scots pine in Sweden (manuscript)

Papers I and II are reproduced with the permission of the publisher.

1 Introduction

Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and loblolly pine (*Pinus taeda* L.) are conifer tree species with wide geographical distributions. Norway spruce and Scots pine are both native and among the dominant species in the mountainous and boreal regions of Europe and Asia, while loblolly pine is native to the temperate south-eastern USA. Norway spruce is a shade-tolerant species, naturally emerging under the canopy of pioneer species on wet and mesic sites or in areas with few forest fires. The species has high demands for water and needs relatively fertile soils to grow well. Scots pine is a pioneer species, naturally growing on dry and mesic sites with frequent forest fires; it grows well even on infertile sites and has a low demand for water. Loblolly pine is a pioneer species, growing well on a range of sites and soils, except those that are very wet or very infertile (Preston & Braham, 2002), although it is generally found in lowlands and moister areas. The species is resistant to fire and is considered a fire subclimax species.

These three species have great importance for forestry over large areas. Norway spruce and Scots pine are the two main naturally occurring species in Swedish forests. Together they constitute about 80 % of the standing volume and each year some 350 million seedlings of these species are planted (Swedish statistical yearbook, 2013). In the south-eastern USA, loblolly pine is the most commercially important tree species. It is dominant across about 13 million ha (Baker & Balmer, 1983; Schultz, 1999) and each year, almost one billion seedlings are planted (McKeand *et al.*, 2003; McNabb & Enebak, 2008).

1.1 Tree improvement

One of the most effective silvicultural tools to increase forest growth is the use of genetically improved material. For Norway spruce and Scots pine in

Sweden, no other silvicultural practice, including fertilization, improved establishment, and planting exotic tree species, is estimated to increase the growth as much as using improved material (Rosvall, 2007; Rosvall & Lundström 2011). The potential for increased growth compared to unimproved plant material, with respect to mean annual increment (MAI), in the current supply of improved plant material for both Norway spruce and Scots pine is in the range of 10-20 % (Rosvall *et al*., 2001). In the near future, this additional growth will increase to 25 % as new seed orchards produce seeds from superior genetic material. Similar or even larger genetic gains are estimated for loblolly pine in the south-eastern USA. Conservative estimates of genetic gain with respect to yield are in the range 10-30 % (McKeand *et al*., 2003; Aspinwall *et al*., 2012).

The objective of tree breeding programs is to improve the profitability of forestry by changing the genetic constitution of the tree populations. Often, this is achieved by improving both tree growth and stem quality traits. Important selection traits in many breeding programs are stem volume growth, disease resistance (White *et al*, 2007) and branch and stem characteristics (Haapanen *et al*., 1997; Li *et al*., 1999; Cameron *et al*., 2012). In traditional tree breeding programs, the frequencies of favorable alleles that influence selected traits are increased by selecting superior individuals that are crossed to form even more superior offspring for selection (White *et al*., 2007). The breeding cycle includes three major activities: testing, selection and crossing to create a new generation to be tested for selection (Figure 1). This is repeated to achieve greater genetic gains over time. For Norway spruce and Scots pine in Sweden, the generation turnover is about 20-25 years (Lindgren, 2009) and is estimated to result in an average genetic gain equivalent to 10 % (Ståhl & Bergh, 2013).

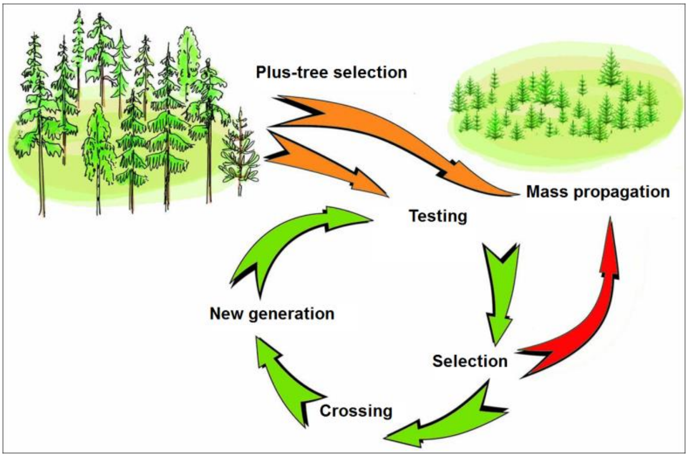

*Figure 1.*The breeding cycle (Ståhl & Jansson, 2000).

Genetic tests are often planted on homogeneous forest sites, although former agricultural land, greenhouses, etc. are also used. However, all such experiments allow separation of genetic and environmental effects. A fundamental concept in forest genetics is the phenotype (P), which consists of both an environmental (E) and a genetic (G) component:

$$\mathrm{P} = \mathrm{G} + \mathrm{E} \qquad (1)$$

The genetic component is heritable, in contrast to the environmental component, and is used to estimate genetic measures and variances. An example is breeding value, which is a measure of the value of an individual compared to the population average judged by the mean value of the individual's progeny. Another important measure which can be estimated from the genetic component is genetic gain, which is the mean progress of an entry compared to unimproved material. Often several field trials at different locations are used to obtain robust estimates of genetic values that are valid under different environmental conditions. Many field tests use small row plots or single-tree plots, in which several genetic entries (provenances, families, clones) are distributed within test units. Single-tree plot designs allow many entries to be tested in a relatively small area, which makes this type of design statistically very efficient and commonly used (Jansson *et al.*, 1998; White *et al.*, 2007). However, single-tree plots can produce biased estimates of growth traits that are affected by competition, favoring entries with initially fast growth, while entries which are initially slow growing are disfavored (Cannel, 1982; Foster, 1992; Vergara *et al.*, 2004; Ye *at al.*, 2010). Ideally, block-plot trials, where a single genetic entry is present in the plot, should be used for traits that are affected by competition (Andersson *et al.*, 2007; Gould *et al.*, 2011). However, this design is often not practical as it requires very large homogenous areas in order to test many entries (White *et al.*, 2007). The most feasible solution, therefore, is to use single-tree plots and to evaluate these before the onset of competition.

Most of the genetic tests are undertaken at an early age, within the first 25-50% of the rotation time (White *et al.*, 2007). Norway spruce and Scots pine in Sweden are evaluated earlier, when they are about 3-5 m tall, which is typically about 20 % of the rotation time (Rosvall *et al.*, 2011). One important objective in tree improvement programs is to increase the volume growth over the whole rotation period. Early genetic evaluations are therefore used as indicators of future volume production (Jansson, 2007). In general, early evaluations have shown good correlation to volume growth per unit area in more mature stands (Butcher & Hopkins, 1993; Callister *et al.*, 2013). For Scots pine in Sweden, Jansson (2007) found a strong correlation (0.8) between height at age nine and volume growth per unit area at age 30 in five genetic trials. In addition, predicted gains have effectively matched realized gains based on block-plots (St. Clair *et al.*, 2004; Vergara *et al.*, 2004; Weng *et al.*, 2008a; Stoehr *et al.*, 2010; Ye *et al.*, 2010; Verryn *et al.*, 2009), indicating rather unbiased predictions from progeny tests using small plots. However, in a study on black spruce (*Picea mariana* [Mill.] BSP) by Weng *et al.* (2011), the realized gain for diameter at breast height (dbh) from block-plots did not match the corresponding gain from progeny test using small plots, which highlights the need to evaluate single-tree plots before the onset of competition. Genetic analysis of field trials allows for selection in which all desirable tree characteristics are combined in a composite breeding objective. The relative contribution of traits like tree height and diameter to the objective are weighted on the basis of their genetic properties and economic value (Magnussen, 1990; Berlin, 2009; Berlin *et al.*, 2010).

Genetic tests are also used to detect genotype by environment interactions (G×E interaction). The essence of a G×E interaction is a lack of consistency in the relative performance of genotypes in different environments (White *et al.*, 2007). The interaction can be due to rank changes (Colbert *et al.*, 1990) or to a non-constant difference in performance in the different environments (White *et al.*, 2007). A G×E interaction may be found for species (Butterfield, 1996) as well as for provenances (Matheson & Raymond, 1986), families (Li & McKeand, 1989) or clones (St. Clair & Kleinschmit, 1986) of the same species. The different environments can reflect the effect of various environmental factors, such as climate, soil fertility or site (Wu & Matheson, 2005), as well as silvicultural factors, such as different planting densities (Stoehr *et al.*, 2010; Aspinwall *et al.*, 2011; Ye *et al.*, 2010), or fertilizer applications (Colbert *et al.*, 1990). When a G×E interaction occurs, the simple model (Eq. 1) is no longer sufficient to explain the observed variation. A more satisfactory model must include the interaction:

$$\mathrm{P} = \mathrm{G} + \mathrm{E} + \mathrm{GE} \qquad (2)$$

1.1.1 Norway spruce and Scots pine tree improvement in Sweden

Sweden was one of the first countries to establish a forest tree improvement program, with organized tree breeding starting in 1936 (Eriksson *et al.*, 2013). An important step in Norway spruce and Scots pine breeding was the large scale selection of plus-trees, which commenced in the mid-1940s. This selection was made in mature and often naturally regenerated stands (Karlsson & Rosvall, 1993; Wilhelmsson & Andersson, 1993). To increase the size of the breeding population, a second round of plus-tree selection was undertaken during the 1970s-1980s. This time, the trees were selected in even-aged, well developed, planted or sown stands at about 1/3-1/2 of the total rotation time. Important selection traits in the first as well as the second round of plus-tree selection were tree height, diameter, vitality, and stem quality (Werner *et al*., 1981). These initial plus-tree selections could only consider the trees´ individual phenotypes.

Subsequently, selection has also been based on genetic information from relatives in well-designed progeny trials. The breeding programs for Norway spruce and Scots pine are now at the stage of moving on from crossing tested and selected founder trees to form the first generation of the breeding population, to forming the second generation.

Today, the objectives of the Swedish long-term Norway spruce and Scots pine breeding initiated in the late 1980s are: (i) conservation of genetic variation; (ii) preparedness for future climate change; and (iii) breeding for general purposes such as increased growth (Danell, 1993). This work is achieved by using a multiple population breeding system, MPBS (Namkoong, 1984; Eriksson *et al*., 1993), which consists of many closed sub populations with different adaptation profiles (Danell, 1993). For Norway spruce and Scots pine, some 20 populations are used for specific climate zones described in terms of photoperiod and temperature climate (Figure 2). Breeding is implemented within each sub population, in which 50 parents are maintained per generation. The selection is made within families and crossing is conducted according to a double-pair mating design (Danell, 1993; Hannrup *et al*., 2007).

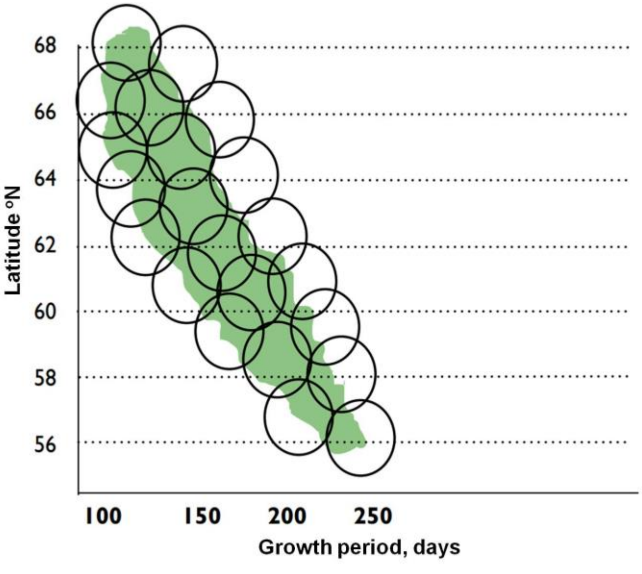

Figure 2. Distribution of breeding populations in Sweden in relation to latitude and growth period (Jansson, 2010). The green area reflects the current growth period in Sweden.

1.1.2 Loblolly pine tree improvement in the south-eastern USA

Like Sweden, the south-eastern USA organized tree improvement programs from an early date. In 1951, the first breeding programs covered Texas, Louisiana and Arkansas (Zobel & Talbert, 1984) and, since then, the working territory has widened to include most of the south-eastern states. The most important selection traits in the program are volume production, resistance to fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*), and stem straightness (Aspinwall *et al.* 2012; Li *et al.*, 1999; McKeand *et al.* 2006). The generation turnover in the improvement program for loblolly pine is short compared to Norway spruce and Scots pine in Sweden, which has allowed the programs to advance relatively rapidly. Today, improvement programs are testing the progeny from the 4th generation of breeding.

1.2 Growth and yield models

Growth and yield models are used to describe, predict and explain the growth of forests. *Growth* refers to the increase in dimension of one or several trees over a given time period (e.g. volume growth in $m^3ha^{-1}y^{-1}$), and is different from *yield* which refers to the final dimension at the end of a specific time period (e.g. m^3ha^{-1}) (Vanclay, 1994). Growth and yield are mathematically related, if y is yield, growth is the derivative dy/dt.

Most models are based on observations collected during surveys of commercial or natural forests or experiments, so called *empirical models*. These models are a standard tool in forest management (Vanclay, 1994) and provide an efficient methodology to forecast resource development and to explore management options and silvicultural alternatives. Growth models can be constructed for a single stand and may produce information about mortality, growth and other changes in stand characteristics during a specific time period (Pretzsch, 2009). However, growth models can also be constructed for individual trees (e.g. height-, diameter- or basal area growth per year). *Individual tree models* are, in general, more detailed and require more information compared to *stand models,* for instance these models often need information about the relative size of the specific tree and sometimes also the spatial position of the neighboring trees (Weiskittel *et al.* 2011). Yield can be estimated by summing individual tree volumes (Burkhart & Tomé, 2012). Growth models can either be *deterministic* or *stochastic*. A deterministic model estimates the expected growth and will always predict the same result if the initial conditions are the same. A stochastic model attempts to simulate natural variation and will provide different predictions depending on particular probabilities. This means that this type of model will seldom predict identical results for repeated runs, but will provide an indication of the probable variation in outcome. These two types of model serve different purposes. A deterministic model is useful when predicting yields and to analyze treatment effects, while a stochastic model is useful to estimate the reliability of the model or when analyzing the risks of different treatments (Vanclay, 1994).

1.2.1 Norway spruce and Scots pine growth models in Sweden

Empirical growth models are commonly used in forest management in Sweden. In recent decades many growth models have been constructed (Eriksson, 1976; Agestam, 1985; Ekö, 1985; Söderberg, 1986; Persson, 1992; Nyström, 2001, Fahlvik & Nyström, 2006). Most of these models involve a number of sub-models and separate the growth of the stand into two stages: establishment and the established period (Elfving, 2010; Fahlvik *et al.*, 2014). Height is the dependent variable in most models during the establishment stage and basal area is the dependent variable for the established stand stage. The transition between these stages normally occurs at a mean height of about 7 m. At this point, heights are commonly converted to basal area using height-diameter models. Since 2009 many of the available growth models have been compiled in the Heureka decision support system. This system enhances analysis and planning of silvicultural treatments and strategies in stands, forests and regions and provides information relating to many values e.g. economic, silvicultural, biodiversity and recreation (Elfving, 2010; Wikström *et al.*, 2011).

However, the empirical growth models in use today are based on old data from permanent sample plots in unimproved stands and the effect of genetic improvements is not explicitly taken into consideration. Since many forests are now genetically improved, the models may produce biased predictions and their application may result in suboptimal forest management. Accurate and appropriate models are becoming more and more important as the area planted with improved material is increasing, as is the genetic gain resulting from the improvement programs in new plantations. There is, therefore, a need to investigate whether the current models need to be adjusted and, if so, what is required in order to predict the growth of genetically improved material correctly.

1.2.2 Incorporation of genetic effects into growth models

One way to incorporate genetic effects into growth models would be to develop new empirical models or refit growth equations specifically for improved material (Gould & Marshall, 2010). However, long-term growth data from genetically improved stands from representative areas of the forest land are often missing and so, in many cases, this approach is not feasible. In addition, as tree breeding continues, new generations of improved material are produced before the previous generation has completed its rotation, leaving the growth modelers constantly one step behind the genetic improvement.

Instead, most studies have focused on how to incorporate increased growth rates into existing growth models. One way is to change the height–age curve to reflect increased height growth rates. In a study on loblolly pine (Buford & Burkhart, 1987) differences were found in the level of the height-age curve between different families (a group of sib trees with common parents), indicating that the development of different families could be modeled by adjusting site index carefully. Similar results were also found again for loblolly pine (Knowe & Foster, 1989) and for maritime pine (*Pinus pinaster* Ait.) (Danjon, 1995). In a study on Hinoki (*Chamaecyparis obtusa* Endl.) by Kurinobu & Shingai (1987), a five year height gain of 5.7 % resulted in an increased site index of 2.6 %, which would generate an increase in stand volume of 6 % (age 60) and 8 % (age 45), compared to unimproved material. However, these estimates assumed that site index does not change over time with improvement level, which may not be true. In a study on loblolly pine by Sprinz *et al.* (1989), the patterns and rates of average height and height growth of the dominant trees over 29 years varied according to seed source. Long-term growth predictions using site index based on very early height measurements could, therefore, be imprecise. Adams *et al.* (2006) found that merely adjusting site index had little effect on projected stand volume. In order to better estimate the future stand volume for genetically improved material, also modifications of other models in the growth simulator were needed, e.g. spacing by family specific survival functions and family specific diameter functions.

Another approach that requires moderate modification of current growth models is to use genetic multipliers. These have been developed and calculated to reflect the relative growth difference between improved and unimproved material (Hamilton & Rehfeldt, 1994; Carson *et al.*, 1999; Gould *et al.*, 2008; Gould & Marshall, 2010). Predicted growth increments from current models are then adjusted using multipliers to account for genetic gain in growth rate. This means that genetic multipliers modify predicted height or diameter while the original function of the model remains unchanged. An advantage with this approach is that estimated genetic gains or breeding values from genetic trials can be included directly in the models without transforming genetic gains to site-index changes. An example of this is the study by Gould *et al.,* (2008) on Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) where genetic multipliers were developed from height and diameter breeding values to improve growth predictions with existing models. Like site index, genetic multipliers may not be constant over time. In a study by Hamilton and Rehfeldt (1994), three genetic multipliers were estimated for the height of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) during the first 19 years. Depending on the time of the evaluation, the genetic multipliers varied between 1.0343 and 1.2111, indicating that the superiority in growth rate of the genetically improved material varied over time. In a study by Carson *et al*. (1999), constant genetic multipliers for height and basal area were used when modeling development for different genetic entries of *Pinus radiata* D. Don. The results indicated that a constant increase in the rate of growth does not necessarily give a constant percentage gain over time. Instead, the predictions showed decreasing percentage gain from age 15 to 40, although the absolute difference between the genetic entries increased during this time. An alternative to using genetic growth multipliers would be to use a time multiplier, where the age of the stand or the tree is adjusted for various genetic entries. Smith *et al.* (2014) concluded, in study on ten open-pollinated loblolly pine families, that a growth multiplier would be sufficient to account for genetic variation for most growth traits. However, for diameter and basal area per hectare, a time multiplier could be applied to existing models to accelerate or decelerate the development.

Besides incorporating increased growth rates into the models, it is also important that the models account for genetic differences in stem slenderness (height-diameter ratio) to give unbiased yield forecasts. Environmental factors and silvicultural treatments largely determine stem slenderness (Kroon *et al*., 2008), although genetic factors may also play an important role (Harrington & De Bell, 1996; Kroon *et al.*, 2008). In a study of Scots pine, plus-tree progeny were shown to be more slender compared to the progeny of unimproved trees (Andersson *et al*., 2007). In a block-plot trial, stem slenderness differences in loblolly pine (*Pinus taeda* L.) were found between improved and unimproved material (Buford & Burkhart, 1987). However, this was merely an effect of differences in the intercept of the height-diameter curves, indicating that if an appropriate site index was chosen there was no need to change the height-diameter ratio when modeling improved material. The improved material was more slender than unimproved material because it grew more rapidly, and thus was exposed to more intense competition in the plots, rather than because of genetic differences in stem slenderness. It is important to note that the trees were analyzed at the same age and not at the same height. Similar results have been found by Weng *et al.* (2008b) in a block-plot trial of Jack pine (*Pinus banksiana* Lamb.) and in a block-plot trial of loblolly pine (Sabatia & Burkhart, 2013). Differences in stem slenderness can also be incorporated into growth models indirectly by using height- and diameter-specific genetic multipliers. In a study by Carson *et al*. (1999), the genetic multipliers for diameter were substantially larger than genetic multipliers for height, which could indicate, depending on the design of the height- and diameter models, that the genetic entries were less slender compared to unimproved material. In a similar study by Hamilton and Rehfeldt (1994), genetic multipliers were estimated to be 1.072 for height and 1.093 for diameter for open pollinated ponderosa pine families. Appropriate genetic multipliers for Douglas-fir genetic entries were estimated to be 1.072 for 10-year height gains of 20 % and 1.092 for diameter gains of 30 % (Gould *et al*., 2008). In general, the variation in genetic multipliers for height and diameter can be explained by differences in height and diameter growth models, as well as by how relatively significant height and diameter were in the genetic selection (Carson *et al*., 1999).

2 Aims of the thesis

The main objective of the research described in this thesis was to analyze important effects of tree improvement on tree growth in order to improve growth models. The specific questions addressed were:

- What are the effects of different genetic entries planted in different densities on growth traits of Scots pine (I) and height-diameter relationships of Loblolly pine (II), respectively?

- Are current height growth models of young stands valid for genetically improved Norway spruce and Scots pine? If not, how do these models need to be adjusted in order to predict the growth better? (III)

- How has plus-tree selection affected the height-diameter ratio of Norway spruce and Scots pine? (IV)

3 Materials and methods

This chapter provides an overview of the materials and methods associated with the four papers. For more detailed information, see the corresponding papers.

3.1 Materials

To answer the questions posed in this thesis, experimental genetic data from trees up to 20 years of age were needed. Therefore, this research had to rely entirely on existing field trials (Papers I-IV). The experiments used in papers III and IV were set up by the Forestry Research Institute of Sweden, SkogForsk, which is the organization that establishes and maintains the genetic field trials of the breeding programs in Sweden. Experiments set up by the Swedish university of agricultural sciences SLU (paper I) and NC state university (Papers II) were also used.

Papers I and II are based on two genotype by environment experiments. The experiment referred to in paper I was established in 1990 by SLU at the Remningstorp estate in south-western Sweden. In each plot, 300 seedlings were planted from each of 30 half-sib families. Three spacings were tested (1×1m, 2×2m and 3×3m) and each spacing was replicated four times. The study analyzed a number of growth and quality traits at different ages. The trial referred to in paper II was established in January 2006 by the NC state university and is located at the Hofmann Forest in Onslow County, North Carolina, USA. The study included nine different genetic entries and two different spacings: 1.5×6.1 m and 3.0×6.1 m replicated in six blocks. The genetic entries included two clones (C2-C3), three full-sib families (FS1-FS3), three open-pollinated families (assumed to be half-sib families, HS1-HS3), and one seed orchard mix (SOM). All of these entries have been used in extensive operational plantings in the south-eastern US and were considered to be of high genetic value.

Papers III and IV are based on 47 single-tree plot progeny trials of both Norway spruce and Scots pine, distributed across large parts of Sweden (Figure 3). These trials were established between 1977 and 1994 to test individual clones or progeny of different plus-trees. These trials were suitable for the work presented in papers III and IV as they were well established and replicated, and represented large variation with respect to the genetic gains within the trials. The trials used in the work described in paper III were located in southern Sweden. Tree height was measured on two occasions up to an average height of about 7 m. The first measurement was made at the age of 7-15 years when trees had attained an average height of 1.3-3.4 m. The second measurement was made at the age of 12-20 years when trees had attained an average height of 2.6-6.9 m. Paper III also used data from the HUGIN young stand survey (Elfving, 1982; Nyström, 2001) to develop individual tree height growth models for unimproved Scots pine and Norway spruce. The data comprised a large number of stands that were established in the period 1950-1965. In the period 1976-79, permanent plots were established in about 800 young stands with a mean height of about 3-4 m, distributed throughout Sweden. In each stand, five circular plots measuring 100 m^2 were randomly sampled. After five years, during the period 1981-1984, the plots were measured again. The trials referred to in paper IV contained progeny from both plus-trees and neighboring trees. Height and diameter were measured on a single occasion at the age of 15-22 years when the mean height was 3.2-8.3 m and the mean diameter (dbh) was 3.0-11.8 cm. Paper IV also used data from the second round of plus-tree selection which was undertaken during the 1970s and 1980s by SkogForsk, who examined even-aged commercial stands over the whole of Sweden (Karlsson & Rosvall, 1993; Wilhelmsson & Andersson, 1993). In total, 308 Norway spruce and 238 Scots pine plus-trees and more than 7500 neighboring trees were examined. These neighboring trees were considered to be genetically unimproved.

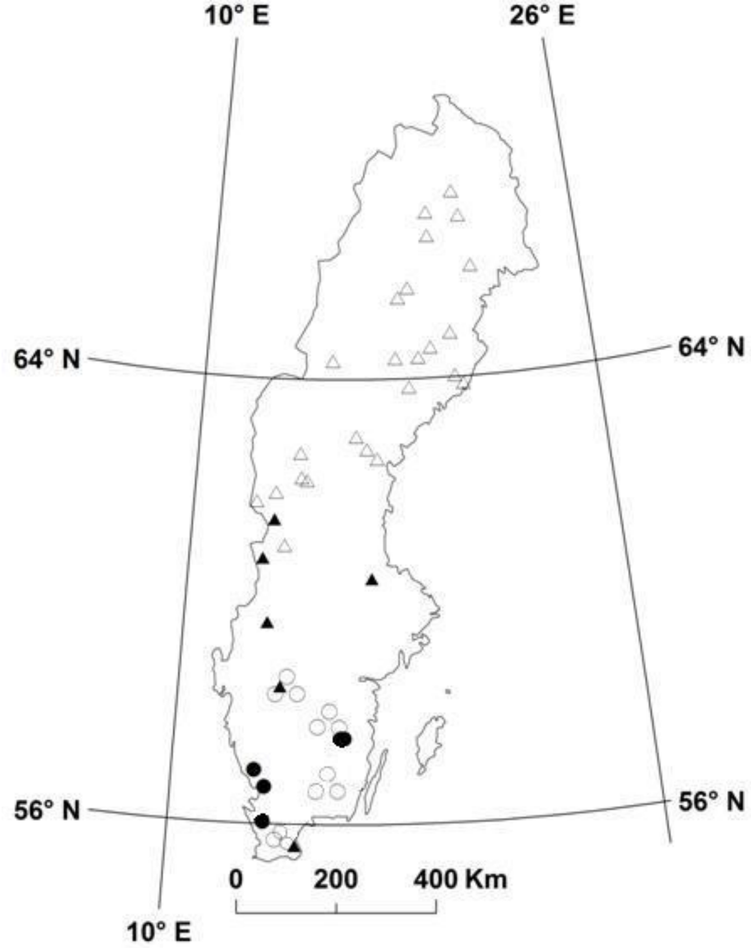

Figure 3. Location of the trials in paper III (filled symbols) and IV (empty symbols) for Norway spruce (circles) and Scots pine (triangles).

3.2 Methods

Mixed model equations (MMEs) were used to estimate genetic components (Papers I-IV) and genotype by environment interactions (Papers I and II). For most field trials, genetic entry was defined as a random effect parameter while block was defined as a fixed effect parameter. These classifications are in line with how these factors are modeled in Swedish and international forest tree breeding (Falconer & Mackay, 1996; Lynch & Walsh, 1998; White *et al*, 2007). Genetic entry is normally treated as a random effect as the entries are considered a be a sample of a larger population and the investigation is often focused on population variance components and the future performance of the entries. For this approach there needs to be a fairly large random sample in order to obtain accurate variance components. The number of genetic entries varied between 83 and 309 in the experiments referred to in paper III, which allowed the use of a random effect. These genetic entries were assumed to be a random sample from the breeding population. As a consequence, the results from the analysis refer to the breeding population and not the total population of the species in Sweden. Since the samples of entries in papers I and II were based on smaller samples of entries, they were classified as a fixed effect. The MIXED procedure in the SAS software (SAS Institute, Inc., 2008) was used in the analysis with the restricted maximum likelihood method (REML).

In papers III and IV, best linear unbiased predictions, BLUPs (Henderson, 1975), were generated for the different genetic entries. BLUPs are commonly used in forest tree breeding because of the way that they handle accuracy. This is because a BLUP, unlike ordinary least squares, is weighted in accordance with the genetic information provided (White *et al*, 2007). This means that less reliable data are regressed towards the average value of the trial, thus, producing more conservative estimates. This is especially important when dealing with unbalanced data. In study III, BLUPs were generated as follows:

$$Y_{ijkm} = \mu + g_{ij} + b_{ik} + \varepsilon_{ijkm} \qquad (3)$$

where Y_{ijkm} is the height (in meters) of tree m belonging to genetic entry j in block k and trial i, μ is the overall mean height, g_{ij} is the random effect of genetic entry j within trial i, b_{ik} is the fixed effect of block k within trial i, and ε_{ijkm} is the residual error. The predicted genetic effect was estimated for each genetic entry within each trial (PGE_{ij}) using the predicted genetic entry deviation from population mean. Each genetic entry was allocated an index according to its genetic performance. Thus, index 0 corresponded to the average performance in the trial. For the half- and full-sib trials, the mean height reflected 10% increased height compared to unimproved material (Rosvall *et al.*, 2001), as these trials consisted merely of plus-tree progenies. In order for PGE to reflect the relationship to unimproved material, the genetic entries had 0.10 added to their estimated PGE values to reflect a 10 % increase from the unimproved level. Similar adjustments were applied to the clone trials, where the mean height reflected 15% increased height compared to unimproved material. In the trials the genetic gain consisted of a provenance effect of 8% (Persson & Persson, 1992) and a selection effect of 7 % resulting from choosing superior clones (Rosvall *et al.*, 2001). Thus, the genetic entries in the clonal trials had 0.15 added to their estimated PGE values.

An important factor to consider in this research was the competition between trees. In papers I, III and IV, single-tree plot trials were used which can produce biased estimates of growth traits that are affected by competition, because fast growing entries are favored while initially slow growing ones are disfavored (Cannel, 1982; Foster, 1992; Vergara *et al.*, 2004; Ye *at al.*, 2010). In paper III this was handled by developing an individual tree model which predicts the height increment of trees in different competitive environments. The model predicts height growth as follows:

$$ih_5 = \exp(\beta_0 + \sum \beta_i X_i) + \varepsilon \qquad (4)$$

where ih_5 is the five year height increment, β_0 is a constant, β_i form a vector of coefficients for the independent variable X_i and ε is a random component. One of the variables is a competition index which decreases the height increment of relatively small trees. Another way of accounting for competition is to study trees that are less affected by competition effects. In paper IV, dominant trees were analyzed, as these are less affected by competition from the surrounding trees and, thus, more appropriate when examining genetic differences in stem slenderness. However, it is not only single-tree plot trials that are affected by competition, the analysis of block-plot trials also needs to consider competition in order to produce unbiased estimates. This is because the competition will be most intense in the plots with the fastest growing genetic entry (Andersson *et al.*, 2007; Correll & Anderson, 1983). Similar to the study described by Buford (1986) and Buford and Burkhart (1987), paper II handled this by using the Korf two parameter height-diameter function (Zeide, 1993) when estimating stem slenderness differences, which enabled these differences to be explained by both the intensity of the competition as well as genetic stem slenderness differences. In study II, the asymptote of the height-diameter function was used as an indicator of site index, while the slope of the height-diameter function indicated genetic stem slenderness differences.

4 Main results and specific discussion

4.1 Family and spacing effects on growth traits and height-diameter relationships

Paper I investigated the reaction of different genetic entries to a variety of plant spacings. The results showed that there were significant differences ($p < 0.05$) among spacings and among families for all growth traits (Table 1). Trees from the 2×2m spacing were tallest at all ages, followed by the trees from the 1×1m spacing. Trees from the 3×3m spacing were shortest at all ages and significantly shorter than the trees from the 2×2m spacing ($p < 0.05$). For diameter and volume at age 21, trees from the 3×3m spacing were the largest and trees from the 1×1m spacing the smallest. In addition, significant interactions were found between family and spacing for all growth traits ($p < 0.05$). This corresponds well to the findings of Ye *et al.* (2010), who reported significant genetic-by-spacing interactions for several growth traits at the ages of 8 and 15 for Douglas-fir. Similar results have also been reported for radiata pine (Beets & Kimberley, 1993; Lin *et al.*, 2013) and loblolly pine (Aspinwall *et al.*, 2011), while Stoehr *et al.* (2010) found no significant interaction for Douglas-fir. The interactions were most obvious at young ages when the spacings provided different competitive environments. Except for spike knots (SK21), no significant interaction was found for the quality traits, corresponding well to the studies of Ye *et al.* (2010) and Lasserre *et al.* (2005).

Table 1. *Observed significance of different variables, based on ANOVA for data from individual trees from paper I.*

Source of variation	df	p-value							
		HT7	HT9	HT21	DBH21	VOL21			
Spacing (S)	2	0.0497	0.0261	0.0171	<.0001	<.0001			
Family (F)	29	<.0001	<.0001	<.0001	<.0001	<.0001			
S x F	58	0.0044	0.0002	0.0425	0.0426	0.0437			
	df	BR21	ANG21	QL21	STR21	SK21		df	DT21
Spacing (S)	2	<.0001	<.0001	0.0660	0.2689	0.0036	Spacing (S)	2	0.0178
Family (F)	9	0.9445	0.0019	0.2339	0.0790	0.0134	Family (F)	8	0.4747
S x F	18	0.8584	0.1631	0.1927	0.2813	0.0131	S x F	16	0.2728

Traits: HT7, HT9, HT21 = height (m) at ages 7, 9 and 21 respectively, DBH21 = diameter (cm) at age 21, VOL21 = volume (dm^3) at age 21, BR21 = branch diameter (mm) at age 21, ANG21 = branch angle at age 21, QL21 = timber quality at age 21, STR21 = stem straightness at age 21, SK21 = occurrence of spike knots at age 21, DT21 = occurrence of double stems at age 21.

Genetic by environment interactions are important to consider. From a silvicultural point of view, the results indicate that family performance may vary in relation to spacing. Therefore, even though general conclusions cannot be drawn from this single location experiment, the results indicate that genetic by environment interactions should be considered when planning the strategy for testing the recruitment populations used for selection. Currently, 2×2m spacing is mostly used for establishing stands, while 1×1m and 3×3m spacings are used less. However, wider spacings may provide a cost saving alternative in the future; thus, more studies are needed to test whether the current results from breeding trials are valid for wider spacings. Wider spacings in genetic field trials would also be positive from a selection point of view. This is because the competition between trees will be delayed, which may enable later selection and higher correlations to whole rotation volume growth. However, wider spacings would demand more extensive field trials which may not be feasible. In addition, increased precision resulting from selecting at an older age may not be worthwhile as this would generate longer generation turnovers in the breeding programs.

This study did not examine the reasons for the interaction, whether it was due to rank changes (Colbert *et al.*, 1990) or to a non-constant difference in performance in the different environments (White *et al.*, 2007). The interaction may have also been caused by a large or limited number of families. More information about the nature of the interaction would have improved the study.

The results presented in paper II, relating to loblolly pine height-diameter data, indicated no significant differences between the non-clonal genetic entries for either the asymptote ($p = 0.1049$) or the slope parameter ($p = 0.2727$) of the height-diameter functions. This means that the samples of seedlings produced by traditional seed propagation methods have similar asymptote and slope parameters. All of these genetic entries are used commercially and grow well, and there is no evidence from this study that any modification of the height-age and height-diameter models is necessary. This is because the asymptote is a good indicator of the height-age relationship, while the slope parameter is a good indicator of the stem form (Buford, 1986; Buford & Burkhart, 1987). These results are in line with the findings of Buford (1986) and Buford and Burkhart (1987), who reported that there was no difference in height–diameter model shapes among nine loblolly pine seed sources; they also support the results of Weng *et al*. (2008b).

However, when analyzing all genetic entries including the two clones, significant differences were found for both the asymptote ($p < 0.0001$) and slope parameter ($p = 0.0060$). Based on these results, it seems possible that the need for more specific models will increase as more genetically homogenous clonal stands are planted. Today, open-pollinated families are the most common planting material in the south-eastern US (McKeand *et al*., 2003; McKeand *et al*., 2008). However, clonal block plantings are becoming more common (McKeand *et al*., 2008), and there may be a need for more genetically specialized height-age and height-diameter models.

Besides genetic effects, this loblolly pine study revealed significant differences ($p < 0.0001$) in the slope parameter due to spacing. This means that spacing affected stem form, making the trees in the denser spacing more slender (greater height-diameter ratio) compared to the wider spacing. All genetic entries became less slender when grown at the wider spacing.

This study used the Korf two parameter height-diameter function (Zeide, 1993) to estimate slope and asymptote parameters for each genetic entry in each block. As a result of this, each genetic entry received six point estimates for the slope and the asymptote parameters, respectively. One disadvantage of this approach was that the variation around each point estimate was not taken into account in the later mixed model. An alternative would have been to incorporate a statistical test directly into the Korf function, as in the studies by Sabatia and Burkhart (2013) and Antón-Fernández *et al.* (2012). However, this would have made the statistical procedure more complicated and less transparent. In addition, the rather large number of replicates (six blocks) ensured that our approach was statistically robust.

4.2 If and how to incorporate genetic growth effects into growth models

The results from papers I and II indicated that growth models need to account for genetics as well as competition effects when predicting the development for various genetic entries.

The first part of the research described in paper III developed height growth models (Eq. 3) for young unimproved stands of Norway spruce and Scots pine, which could account for competition effects. When analyzing genetically improved material it was found that the model, as parameterized for the unimproved material, could predict the height increment relatively well for Norway spruce trees with different genetic gains (Figure 4). However, for Scots pine, most entries were predicted to have similar height increments resulting in differences in mean height between the entries that were too small. The models use an initial state to predict a future state; in this case, initial height, total age, distance-independent competition index and site index were used to predict future height. When applying the model to improved Scots pine trees, the initial state no longer provided enough information to forecast future development realistically.

To create a more realistic difference between the entries, a genetic component was incorporated into the growth model and this significantly ($p < 0.0026$) improved the height increment predictions for Scots pine (Figure 4). The genetic component, which minimized the residuals, was estimated to be 0.3207 × PGE. The predicted genetic effect (PGE) is a measure of the entries genetic gain in relation to unimproved material. This approach corresponds well to similar studies where genetic multipliers have been estimated and used (Hamilton & Rehfeldt, 1994; Carson *et al.*, 1999; Gould *et al.*, 2008; Gould & Marshall, 2010). The PGE was estimated for each genetic entry within the trial and resembles genetic gain. In practice, this means that when modeling a genetic entry with a genetic gain equivalent to 25 %, the genetic component becomes 0.08 (0.3207 × 0.25), thus, the height increment is multiplied by 1.083 (exp(0.08)). This means that for any genetic entry with a PGE greater than 0, the height increment is increased.

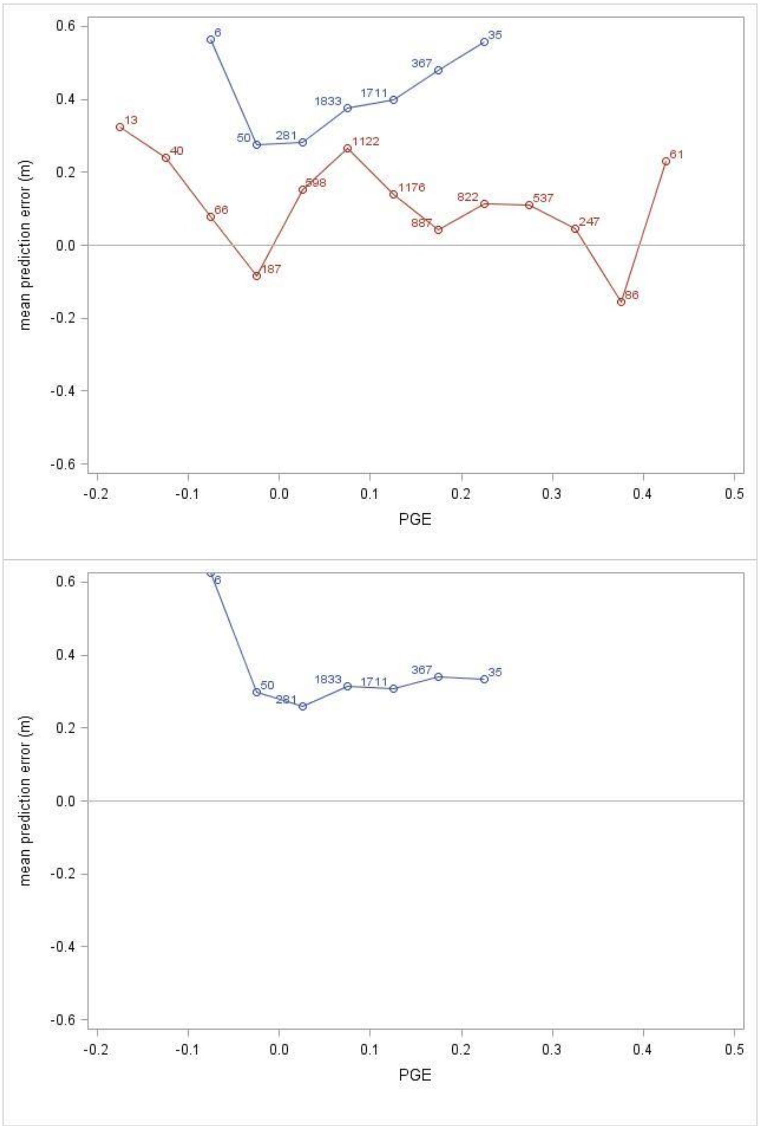

Figure 4. Mean prediction error (m) for the unadjusted (upper panel) and adjusted (lower panel) growth models for Scots pine (blue) and Norway spruce (red) plotted against predicted genetic effect (PGE). The numbers in the graph represent the number of trees in each PGE-class. N.B. The Norway spruce model was not adjusted so this species is missing from the lower panel.

Although a genetic component was needed for Scots pine, some of the information for predicting the height increment of genetically improved material was found in the initial height. This is because initial height was used as a variable for explaining the height development for the coming five-year period. For many young stand simulations using individual tree models, phenotypic tree data are not available for heights of 2-3 m, which is the point that the current model (Eq. 3) starts. Thus synthetic stand data, i.e. a realistic tree height distribution, also has to be generated for improved material (Spirek *et al.*, 1981; Janssen & Sprinz, 1987; Carson & Hayes, 1998; Weng *et al.*, 2010). The results presented in paper III indicate that a genetic entry's initial mean height should be adjusted based on its PGE when synthetic stand data are generated, as PGE is a measure of the genetic gain at the first measurement. Further studies are, however, needed to investigate the distributions around the mean height for genetically improved Norway spruce and Scots pine.

4.3 Effects of plus-tree selection on height-diameter ratio

The results presented in paper IV, derived from measurements of plus-trees in the original stands at the time of selection, indicated that the plus-tree selection significantly favoured phenotypically less slender trees of Norway spruce (-3.2%) and significantly more slender trees of Scots pine (+2.7%) compared to neighboring trees.

When analyzing the genetic component of the phenotypic plus-tree slenderness using progeny data from field experiments, the results indicated that there was almost no difference (-0.2%) in slenderness between the plus-tree progeny and progeny of neighboring trees of Norway spruce. Thus, the observed phenotypic difference in slenderness between plus-trees and neighboring trees in the original stands was almost always only an effect of the surrounding environment. In contrast to Norway spruce, the progeny of Scots pine plus-trees were more slender (+1.7%) than the progeny of neighboring trees. This indicates that the phenotypic differences in slenderness between plus-trees and neighboring trees were partly due to genetic differences. These results correspond fairly well to a similar study by Andersson *et al.* (2007), in which improved Scots pine had a 5.5 % greater height-diameter ratio than unimproved material.

In this study, the heritability of height-diameter ratio was estimated to be 0.22 for Scots pine, which is the same as the value reported by Kroon *et al.* (2008). The value for Norway spruce was 0.38. The moderate heritabilities indicate that environmental factors influence the height-diameter ratio more than genetics, as indicated by the findings reported in paper II, where spacing affected the stem form more than genetics. As in paper II, this study needed to remove competition effects when analyzing height-diameter relationships for various genetic entries. This was achieved by only studying the dominant trees as these are less affected by competition and therefore better reflect the genetic height-diameter relationship. It would have been preferable to take account of competition effects by using a height-diameter function, as in paper II, which would have made it possible to use all trees in the analysis. However, this was not possible because the experiments in this study were designed as single-tree plot experiments with few replicates in each block.

Like the findings of Kroon *et al.* (2008), our results indicate that selecting for height will result in more slender trees of Scots pine but not Norway spruce (Figure 5). The correlation between breeding values of height-diameter ratios and height was low (0.10) but significant ($p < 0.0001$). Thus, current Scots pine breeding programs need also to select for diameter to retain the same height-diameter ratio for improved material as for unimproved material. However, keeping the same height-diameter ratio as unimproved material may not necessarily be optimal. Instead, there may be silvicultural and commercial reasons for selecting for a different height-diameter ratio. Trees with low height-diameter ratios, for example, could be a silvicultural option to reduce the risk of storm and snow damage (Cremer *et al*., 1983; Lohmander & Helles, 1987; Harrington & DeBell, 1996). The corresponding correlation between breeding values of height-diameter ratios and height for Norway spruce was -0.16 and significant ($p = 0.0135$), which indicates that selecting for height would generate less slender Norway spruce trees (Figure 5). It is important to note that even though the correlation between breeding values of height-diameter ratios and height was significant for both species, the low correlation coefficients raise the question of whether selection for height would have any practical consequences on the height-diameter ratio. For Scots pine and Norway spruce, the correlation between breeding value for height-diameter ratio and diameter was -0.85 ($p < 0.0001$) and -0.90 ($p < 0.0001$), respectively, indicating that selecting for diameter would generate less slender trees (Figure 5).

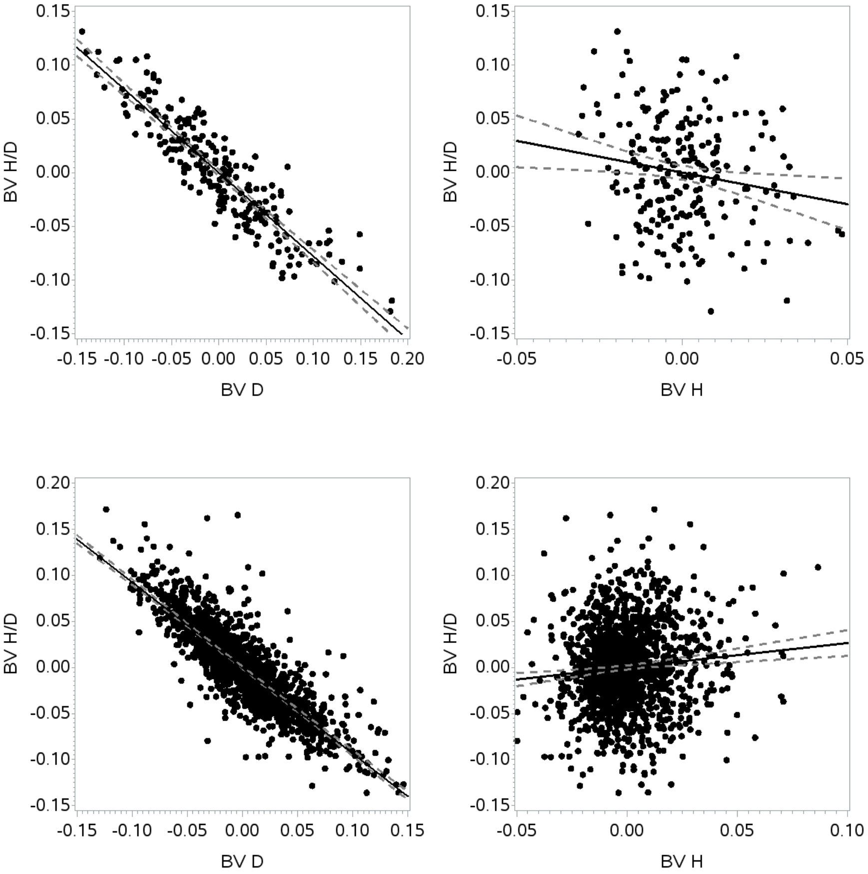

Figure 5. Estimated breeding values (BV) for height (H), diameter (D) and height-diameter ratio (H/D) for Norway spruce (upper panels) and Scots pine (lower panels) including regression lines (black lines) with confidence interval (grey dotted lines).

5 General discussion

The main objective of the research described in this thesis was to analyze effects of tree improvement on tree growth and study the need to adapt growth models to optimize forest planning and management. In general, for all four papers, environmental factors such as planting densities and local conditions affect tree growth more than genetics. Nonetheless, genetic constitution does play an important role as well. The widespread use of genetically improved material of the species studied highlights the fact that even small effects on tree growth may lead to large effects at the whole forest level.

As a basis for optimizing management, it is necessary to have accurate growth and yield forecasts that take genetic improvement into consideration. In general for Swedish forestry, genetic gains are currently not taken into account in growth models and this may lead to delayed operations with reduced profitability. The few examples of incorporation of genetic effects into growth models in Sweden (Rosvall & Wennström, 2008; Simonsen *et al.* 2008) have been based on the assumption that early genetic gains in height, measured in single tree trials, are representative of the genetic gain in areal production over a full rotation, by considering the corresponding changes in site index. Even though there are studies which support this assumption (Butcher & Hopkins, 1993; St. Clair *et al.*, 2004; Vergara *et al.*, 2004; Jansson, 2007; Weng *et al.*, 2008a; Stoehr *et al.*, 2010; Ye *et al.*, 2010; Verryn *et al.* 2011; Callister *et al.*, 2013), this may not be entirely correct. The research described herein did not make such assumptions. Instead, early genetic gain estimates were used in a genetic component that was incorporated into an existing growth model, thus reducing the prediction errors of the growth model (paper III). Consequently, the results from the work presented in this thesis may help to generate more reliable growth and yield forecasts in Swedish forestry and to optimize forest management.

The results presented in this thesis could be incorporated into the Heureka decision support system, which is commonly used and has been able, in general, to generate valid predictions (Fahlvik *et al.*, 2014). Thus, Heureka could be used to analyze the impact of increased height growth in young stands (paper III) and slenderness differences (paper IV) over a full rotation period. A crucial part of such predictions would be examining if and how to incorporate other effects resulting from using genetically improved material, in addition to those presented in papers III and IV. Survival (Olsson & Ericsson, 2002; Persson & Andersson, 2003) and height distribution (Spirek *et al.*, 1981; Janssen & Sprinz, 1987; Carson & Hayes, 1998; Weng *et al.*, 2010) for genetically improved material may also be needed to be taken into account in order to model development over a full rotation correctly. It is also important to bear in mind that the work presented in this thesis only focuses on young forests up to 20 years of age. More studies are needed to analyze and model the growth development in older stands. Preferably, large block-plot trials should be used for these studies as they are easier to analyze with respect to competition effects, compared to single-tree trials. In addition, as tree breeding continues, large block-plot trials are needed to verify genetic gains estimated from progeny trials.

A challenging task in science is to find suitable data to test a number of hypotheses and, in this sense, the work presented in this thesis is no exception. Paper III, for instance, would have been improved if a greater number of trials could have been used. In total, five Norway spruce trials and six Scots pine trials matched the demanding data requirements and consequently, the individual trials had a rather large effect on the results. Random factors, such as imprecise site indices for the trials may, therefore, have exerted a large influence. The greatest obstacle was to find trials where all tree heights were measured twice at an interval of exactly five years. Despite the limited and incomplete data, the work presented in paper III is the first impartial attempt to incorporate genetic gains into growth models in Sweden and will probably enhance growth predictions for genetically improved material. Similarly, paper IV would have been improved if the genetic entries were placed in a larger block-plot as this would have made it possible to use a height-diameter function (as in paper II) to reduce the impact of competition effects. However, large block-plots would have made it impossible to test so many genetic entries, which would have made the estimates more uncertain. Compared to similar studies within this scientific field, the data in papers III and IV represent a very large quantity of material comprising a vast number of genetic entries with many replicates. In addition, the trees in these studies were carefully established and measured, which ensured reliable data.

A persistent issue was how to relate to site index in this thesis. Normally, site index is used as a measure for the productivity of the site and is based on the height of the dominant trees at a specified age. An effect of using genetically improved material is that site index and productivity changes depending on the genetic material growing at the site. Thus, the site index for a newly established stand will probably not be the same as for the previous stand at the site, which means that historical site index data may need to be updated for each rotation at each specific site. In paper III however, site index was estimated from site properties (Hägglund & Lundmark, (1977), which avoided this measure being sensitive to the genetic material planted at the site. The genetic gain was instead incorporated by using a genetic component reported in relation to unimproved material. With this approach, genetic gain did not need to be translated into site index changes, which could become rather difficult in the future as the site index associated with a previous rotation may not necessarily represent unimproved material. The question of what is a correct baseline may become difficult in the future when using site indices based on height and age. However, a problem with estimating site index from site properties is that this is a less precise measure and often tends to underestimate the value compared to figures based on dominant height and age. An example here is the general under-prediction for the Scots pine stand in paper III, which may have been caused by this phenomenon. Thus, there is a need for a more precise way of estimating site index, which would also be applicable to individual stands. One possibility would be to add information to the site index from digital records of soils, location (altitude, longitude, latitude, slope, aspect etc.), temperature, precipitation, radiation, etc. by using geographic information systems.

The growth of genetically improved material also raises a question about the mechanisms behind the growth increase relative to unimproved material. Growth, like other quantitative traits, is regulated by a vast number of genes which makes it difficult to define whether it is caused by differences in growth efficiency, vitality, allocation of growth, growth length during the year or something else. The current hypothesis is that all components are involved. However, better knowledge about the mechanisms behind the increased growth of improved material could be of great value when growth models are constructed or adjusted, as a more specific genetic component could be developed. If, for instance, the genetic gain could be explaned by an increased growing period during the year, latitude or temperature sum could be used to adjust for genetic gains in a growth model. Similarily, if the genetic gain was due to differences in allocation causing the genetically improved trees to produce more stem wood than roots or branches, specific allocation models could be developed for genetically improved material. More knowledge about the mechanisms behind genetic gain would be of even greater importance for process-based models.

The phenotypic plus-tree selection conducted during the 1970s and 1980s, which was studied in the research underlying paper IV, had little genetic impact on the height–diameter ratio for Norway spruce and Scots pine. However, the moderate heritability of height–diameter ratio for both species indicates that breeding can modify this trait, given that the variation is sufficiently large. More studies are needed to investigate the effect of continuous genetic selection on the height–diameter ratio of both species. Depending on the results from such studies, there may be a need to adjust current height–diameter models to predict the growth of genetically improved Norway spruce and Scots pine correctly. Breeding programs could also consider the consequences by adjusting the height–diameter ratio for these species to improve both growth and resistance to wind and snow.

The work presented in papers III and IV concentrated on Norway spruce and Scots pine. However, active improvement programs are also carried out for lodgepole pine (*Pinus contorta*) and silver birch (*Betula pendula*) in Sweden and there may be a need to incorporate genetic gains in growth models for these species as well.

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