Quantitative Genetics of Norway Spruce in Sweden

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Doctoral Thesis
Swedish University of Agricultural Sciences
Umeå 2016

Acta Universitatis agriculturae Sueciae
2016:55

Cover: A 23-year-old Norway spruce progeny trial in southern Sweden, increment core sampled for measuring wood quality traits, and the trend of profitability and stiffness (MOE), and diameter based on different economic weights.
(Photo: Zhi-qiang Chen)

ISSN 1652-6880
ISBN (print version) 978-91-576-8612-1
ISBN (electronic version) 978-91-576-8613-8

Print: Arkitektkopia, Umeå 2016

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Abstract

Genetic improvement of solid wood and pulp and paper products related wood quality traits are important to increase productivity and value of Norway spruce plantation in Sweden. To incorporate wood quality traits into Norway spruce tree breeding program, genetic parameters of solid wood and fibre traits were investigated in a large Norway spruce population. 524 half-sib families from two trials tested in southern Sweden were selected to characterise the genetic variation in wood density, microfibril angle (MFA), modulus of elasticity (MOE), radial fibre width (RFW), tangential fibre width (TFW), fibre wall thickness (FWT), fibre coarseness (FC), and fibre length (FL).

To rapidly measure stiffness (MOE) of standing trees and accurately measure FL from increment cores, a new non-destructive method for quantifying stiffness and a new algorithm for calculating FL were developed. A combination of Pilodyn and acoustic Hitman measurement was found to predict stiffness of standing tree accurately and the new algorithm using Expectation-Maximization could accurately estimate FL.

To improve the estimate of genetic parameters and understanding genotype by environment (G×E) interaction in Norway spruce, spatial analyses were applied to 145 progeny trials and factor-analytic method was applied to 20 half-sib progeny trials. Spatial analysis significantly improved heritability and accuracy of breeding value prediction. Frost damage may be a main driver for G×E interaction for tree height of Norway spruce in southern and central Sweden.

Wood quality traits showed higher heritability than growth traits. However, growth traits had highly unfavourable genetic correlations with solid wood quality traits (0.54-0.75) and weakly to moderately unfavourable genetic correlations with fibre property traits (0.11-0.49).

In conclusion, selection based on diameter alone would have considerable negative effects on wood quality traits, a negligible or small negative effect on FL, and only a moderate effect on FWT. A selection index combining diameter and stiffness, which would have minimal impact on FL, is recommended for spruce breeding. Adequate economic weights for growth and stiffness traits should be determined for Norway spruce breeding program to maximize economic gain for Norway spruce.

Keywords: wood quality traits, growth traits, genetic parameters, age-age correlation, selection index, spatial analysis, factor analytic model, G×E interaction

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Dedication

To my teachers and parents

In God we trust, all other we must bring data.
W. Edwards Deming

Contents

List of Publications

I Chen, Z.-Q., Gil, M.R.G., Karlsson, B., Lundqvist, S.-O., Olsson, L. & Wu, H.X. (2014). Inheritance of growth and solid wood quality traits in a large Norway spruce population tested at two locations in southern Sweden. *Tree Genetics & Genomes,* 10(5), pp. 1291-1303.

II Chen, Z.-Q., Karlsson, B., Lundqvist, S.-O., García Gil, M., Olsson, L. & Wu, H. (2015). Estimating solid wood properties using Pilodyn and acoustic velocity on standing trees of Norway spruce. *Annals of Forest Science*, ss. 1-10.

III Chen, Z.-Q., Karlsson, B., Mörling, T., Olsson, L., Mellerowicz, E.J., Wu, H.X., Lundqvist, S.-O. & Gil, M.R.G. Genetic analysis of fiber dimensions and their correlations with stem diameter and solid wood properties in Norway spruce (submitted).

IV Chen, Z.-Q., Abramowicz, K., Raczkowski, R., Ganea, S., Wu Harry, X., Lundqvist, S.-O., Mörling, T., de Luna Sara, S., García Gil María, R. & Mellerowicz Ewa, J. (2016). Method for accurate fibre length determination from increment cores for large-scale population analyses in Norway spruce. *Holzforschung*.

V Chen, Z.-Q, Helmersson, A., Westin, J., Karlsson, B. & Wu, H.X. Efficiency of using spatial analysis for Norway spruce field tests in Sweden (manuscript).

VI Chen, Z.-Q., Karlsson, B. & Wu, H.X. Patterns of additive genotype by environment interaction in tree height of Norway spruce in southern and central Sweden (manuscript).

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1 Introduction

1.1 Norway spruce breeding in Sweden

Norway spruce [*Picea abies* (L.) Karst.] is one of the most important conifer species for commercial wood production and ecological integrity in Europe (Hannrup *et al.*, 2004). The harvested timber is mainly used either as construction material or for pulp production. Selection of plus trees and establishment of Norway spruce seed orchards to improve the stock started in the 1940s in Sweden (Werner & Danell, 1993). Initially, about 900 plus trees were selected for 10 potential breeding zones. Seed orchards covering about 224 hectares were established using these plus trees. Progeny testing of the plus trees started in 1971 (30 years after plus tree selection). For southern Sweden it was found that the best basal material for breeding originated outside Sweden. During the mid-1970s a large clonal testing program was launched, including more than 18,400 clones, mainly selected from nurseries and mostly of foreign origin. At the same time, a second round of plus trees selection was started, mainly based on selection from the planted stands (a few trees in old progeny trials or provenance trials were also selected) at ages of 20-40 years. In total about 6100 plus trees had been selected by the early 1990s. The 24,500 tested clones and selected plus trees were intended to serve as a founder population for long-term Norway spruce breeding and conservation (Danell, 1993). Material for the Swedish breeding program was organized into 22 partly overlapping latitudinally and longitudinally distributed breeding populations (targeted for breeding zones shown in Figure 1) based on the clinal variation in photoperiod and temperature (Rosvall *et al.*, 2011). The breeding strategy was based on clonal testing and a double pair-mating design as shown in Figure 2 (Lindgren, 2009; Rosvall *et al.*, 1998).

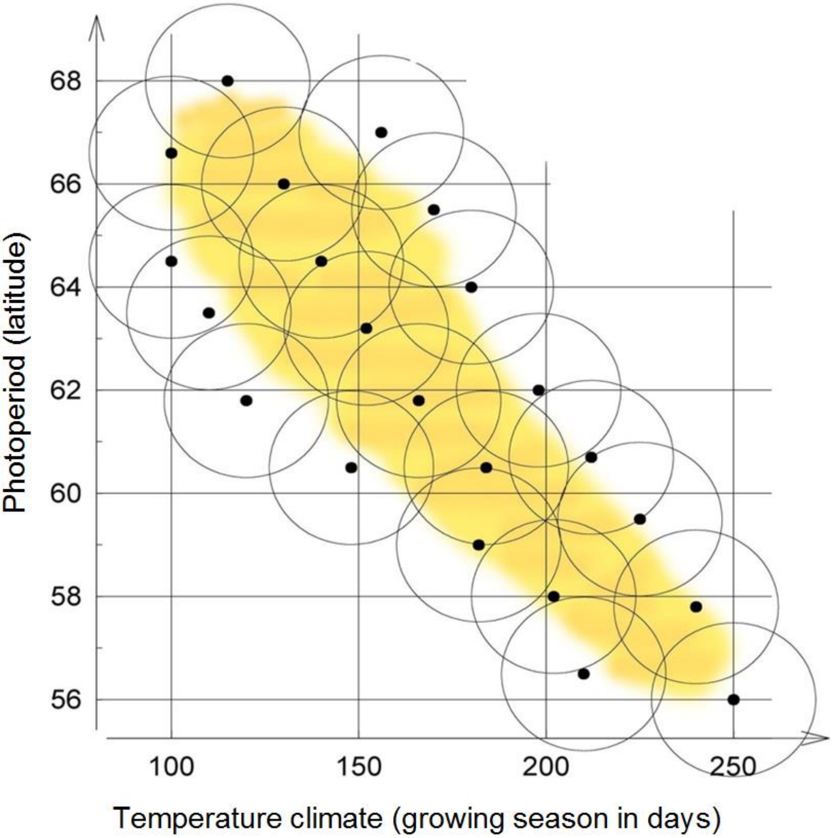


Figure 1. Breeding zones of Norway spruce in Sweden

Norway spruce breeding cycles in Sweden were expected to take 20 years (Karlsson & Rosvall, 1993), starting with selection of 50 superior clones (parents) for each of the 22 populations, and mating each parent with two other parents to create 50 full-sib families. Forty clones per family were used for testing with 14 rooted cuttings of each clone, tested at four sites within their respective (or adjacent) breeding zones. The best clone from each family was selected for inclusion in the next breeding cycle after field testing.

The current Norway spruce breeding program in Sweden mainly focuses on improving growth and adaptive traits, such as height, diameter and survival (Rosvall *et al.*, 2011), and three rounds of seed orchards have been established (the third began in 2000) using progressively improved material (Almqvist *et al.*, 2010). However, unfavourable genetic correlations between growth and wood quality traits such as wood density, modulus of elasticity (MOE), and microfibril angle (MFA) have been observed in several studies in recent years (Gräns *et al*., 2009; Hannrup *et al*., 2004; Skrøppa *et al*., 1999; Steffenrem *et al*., 2009).

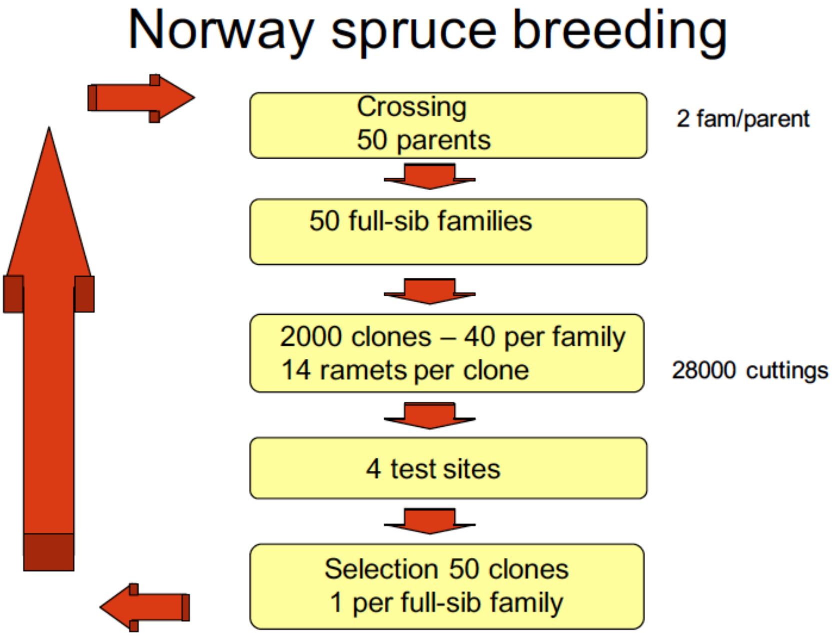


Figure 2. Norway spruce breeding strategy in Sweden

Wood quality traits are key determinants of its economic value. Thus, to improve the economic value of Norway spruce breeding and deployment populations in Sweden, wood quality traits should be incorporated into the selective breeding program. To do so, both non-destructive evaluation (NDE) methods for assessing wood quality traits of standing trees and knowledge of relevant quantitative genetic parameters in the large breeding populations are required. Norway spruce breeding and deployment (seed) zones were mainly developed according to geo-climatic data, as discussed above, and to justify such division of breeding and seed zones, biological data should be used to examine genotype by environmental (G x E) interactions across the zones. Most progeny trials in the Swedish tree breeding program were established using an experimental design with large incompletely randomised blocks or complete randomization, and post-blocking has usually been applied in genetic analyses of field data (Ericsson, 1997). There is a great interest in improving the genetic analyses using more advanced analytical methods. Thus, in the studies this thesis is based upon, reported in the six appended papers (I-VI), improved methods were developed to measure wood stiffness and fibre length (FL), and to estimate quantitative genetic parameters for wood quality traits to incorporate in the Norway spruce breeding program. In addition, advanced spatial analysis and factor analytic models were applied to trials across breeding and seed zones to characterize G×E interaction patterns and improve estimation of both genetic parameters and breeding values.

1.2 Wood quality traits in conifer breeding

Wood quality traits are important because they affect the quality of all kinds of final wood products, such as structure boards, pulp and paper products, and furniture (Zobel & van Buijtenen, 1989). An important division in these products (and hence key traits, as described below) is between solid wood products and pulp and paper products.

1.2.1 Solid wood traits

Wood stiffness (generally expressed in terms of the modulus of elasticity: MOE) is one of the most important traits for construction timber and is mainly determined by measuring wood density and MFA (Baltunis *et al*., 2007; Chen *et al*., 2014; Lenz *et al*., 2011). Genetic variation of wood quality traits was firstly analysed in clonal radiata pine (*Pinus radiata* Don) in the 1950s (Fielding, 1953). Heritability was first estimated for wood density (Dadswell *et al*., 1961; Fielding & Brown, 1960), and in the 1970s and 1980s many studies addressed the inheritance of wood density and related wood traits (Zobel & Jett, 1995; Zobel & van Buijtenen, 1989). Narrow-sense heritability of core density in several major conifer species is usually about 0.5 to 0.8, while the G×E interaction for wood quality traits is generally low according to many studies (Apiolaza, 2012; Baltunis *et al*., 2010; Gapare *et al*., 2010). The genetic correlations between wood density and growth have also been examined in many conifer species. These correlations reportedly vary from negative to positive in maritime pine (*P. pinaster* Ait.) (Bouffier *et al*., 2008; Louzada, 2003; Pot *et al*., 2002), are mostly negative, but weak in loblolly pine (*P. teada* L.) (Bridgwater *et al*., 1983; Gwaze *et al*., 2001; Gwaze *et al*., 2002), and highly unfavourable in radiata pine (Baltunis *et al*., 2007; Wu *et al*., 2008), Scots pine (*P. sylvestris* L.) (Hong *et al*., 2014), and both Norway and white spruce [*P. glauca* (Moench) Voss] (Hylen, 1997; Lenz *et al*., 2011; Steffenrem *et al*., 2009). Such unfavourable genetic correlation makes simultaneous improvement of both growth and wood quality traits in a breeding program challenging (Wu & Sanchez, 2011; Yanchuk & Sanchez, 2011), and has driven shifts in breeding objectives for radiata pine (Ivković *et al.*, 2006) and Scots pine (Berlin *et al.*, 2010), as well as the formulation of alternative breeding strategies for various species (Hallingbäck *et al.*, 2014).

1.2.2 Pulp and paper-related traits

In conifer species, the dimensions of individual fibres, including FL and fibre wall thickness (FWT) strongly affect various pulp and paper properties (Kibblewhite, 1999; Riddell *et al.*, 2005). In addition, the radial fibre width (RFW), tangential fibre width (TFW), and fibre coarseness (FC) are important traits contributing to overall fibre quality (Scallan & Green, 1974). Large genetic variation in fibre traits has been observed in several species (Ivkovich *et al.*, 2002; Shelbourne *et al.*, 1997; Zobel & Jett, 1995). Several studies have also shown that RFW, TFW, and FWT influence wood density (Hannrup *et al.*, 2004; Hong *et al.*, 2014; Lenz *et al.*, 2010), although density is reportedly more strongly genetically correlated with FWT than with either RFW or TFW in Scots pine (Hong *et al.*, 2014), but more strongly correlated with RFW than with FWT in latewood of white spruce (Lenz *et al.*, 2010).

RFW, TFW, and FWT in wood samples can be routinely and automatically measured using a SilviScan instrument (Evans, 1994; Evans, 2006). However, FL is more difficult to measure automatically without measurement bias, mainly because currently available instruments (such as Kajaani Fiber Length Analyzers) cannot distinguish between intact and broken fibres (Svensson & Sjöstedt-de Luna, 2010; Svensson *et al.*, 2006), thus they typically provide a fibre length distribution with two peaks (Mörling *et al.*, 2003). In contrast, distributions obtained from microscopic observations only have one peak (Figure 3). To correct such bias, in the studies this thesis is based upon my colleagues and I (hereafter we) developed a new algorithm accounting for the probability of fibres being broken in increment cores used to measure FL (Chen *et al.*, 2016).

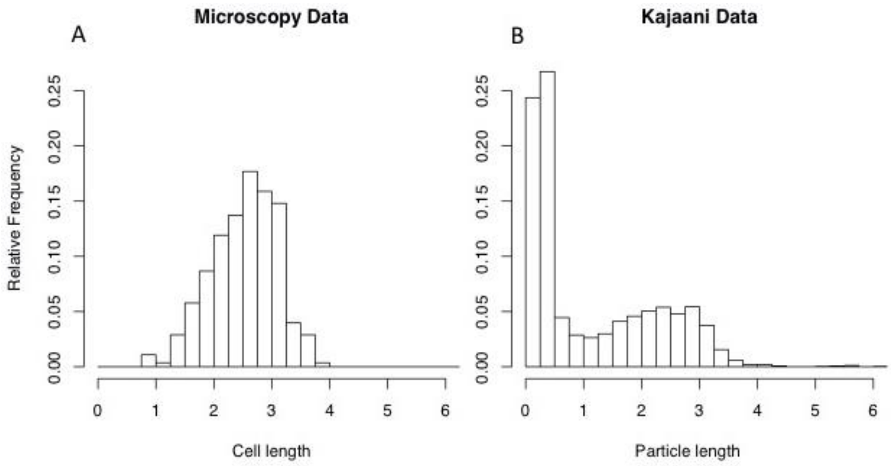


Figure 3. Example of fibre length distributions based on microscopy data representing uncut fibres (A) and on Kajaani data representing cut and uncut fibres and parenchyma cells (B) obtained from the same macerated wood sample.

1.3 Non-destructive Evaluation methods for solid wood traits

Solid wood traits such as wood density, MFA, and MOE are the most important mechanical properties of wood for structural wood products, including construction timber (Hannrup *et al.*, 2004; Zobel & Jett, 1995; Zobel & van Buijtenen, 1989), and are thus the most important traits for selection in tree breeding targeting the improvement of structural products (Evison & Apiolaza, 2015; Ivković *et al.*, 2006). However, traditional measurements of these traits are either expensive or destructive, particularly for MFA and MOE. Therefore, development of methods for rapidly screening standing trees is highly desirable (Matheson *et al.*, 2008). Earlier conifer breeding programs mainly focused on increasing growth rates and hence reducing rotation ages of plantation tree species. Such reduction of rotation age has resulted in increased proportions of juvenile wood in harvested trees, which has lower density, higher MFA, and lower MOE than latewood. Thus it has reduced end-products' values (Wu *et al.*, 2008) and it is important to quantify genetic variation and genetic correlation between growth and wood quality traits in order to formulate closer to optimal breeding strategies.

Mechanical testing of solid wood quality traits requires felling of trees. Further, the preparation of test specimens and the tests themselves are time-consuming and expensive. Wood density is commonly determined by the Maximum Moisture Method, which is much faster and can be used with batches of samples (Smith, 1954). In addition, detailed data on radial variations of numerous solid wood traits (including density, MFA, and MOE) can be obtained using a SilviScan instrument (Evans, 2006; Evans, 1994), and are frequently used as benchmarks to estimate wood properties from increment cores (Chen *et al.*, 2015; Kennedy *et al.*, 2013; Vikram *et al.*, 2011). Using a SilviScan instrument is much more efficient than traditional methods, but the sample preparation and measurements involved are too time-consuming and expensive for scanning samples from thousands of trees included in tree breeding programs (Wessels *et al.*, 2011). NIR (near-infrared) technology could also potentially provide attractive options, but only if reliable prediction models are developed (Schimleck & Evans, 2004; Schimleck *et al.*, 2001).

Several instruments have been developed to estimate wood density in a standing tree indirectly without sample extraction, or at least to rank trees for breeding selection. Examples are the Pilodyn wood tester, Torsiometer, and Resistograph, which have been proposed to replace standard wood density methodology (Isik & Li, 2003; Wessels *et al.*, 2011). The Pilodyn is commonly used to estimate the density of standing trees, and strong genetic correlations (generally -0.80 to -0.95) between Pilodyn readings and standard wood density measurements of several conifers have been reported (Cown, 1978; Fukatsu *et al.*, 2011; King, 1988; Sprague *et al.*, 1983; Yanchuk & Kiss, 1993). However, the Pilodyn can only measure the wood density in the outermost annual rings (close to the bark) so it may be unreliable for ranking individual trees in terms of wood density in whole cores or stem cross-sections (Wessels *et al.*, 2011). Isik & Li (2003) proposed that the Resistograph may be a more effective alternative tool for assessing wood density in standing trees.

MFA is one of the most important wood properties in tree breeding, due to its influence on mechanical properties (Lindström *et al.*, 2004; Zobel & Jett, 1995), but it has debatable effects on properties of mature wood (Cown *et al.*, 1999). Direct microscopic measurement of the variable in individual fibres is extremely time-consuming and expensive, and the representativeness of the results is disputable unless very large numbers of fibres are examined. However, acoustic velocity (AV) measurements with a Hitman ST 300 device could efficiently provide indirect estimates of MFA according to several authors (Grabianowski *et al.*, 2006; Lenz *et al.*, 2013; Li *et al.*, 2007). AV measurements could also provide estimates of MOE (the most important trait for construction timber, and hence target of intense efforts to develop efficient NDE measurement methods), using the following equation:

$$\mathrm{MOE_D} = v^2 * \mathrm{d}$$

where $\mathrm{MOE_D}$ is the dynamic modulus of elasticity (in GPa), v is the acoustic velocity ($\mathrm{km{\cdot}s^{-1}}$), and d is the green wood density ($\mathrm{kg{\cdot}m^{-3}}$). Such estimates of MOE are usually referred to as time-of-flight MOE (Bucur, 2006).

Acoustic methods have been developed for use on standing trees, and for both sorting logs and grading boards in sawmills. Several instruments have been developed for acoustic NDE (Carter *et al.*, 2005; Wang, 2013; Wang *et al.*, 2007), and use of acoustic NDE techniques has been well documented for assessing stiffness of boards from many species, such as Scots pine (Auty & Achim, 2008), Sitka spruce (*P. sitchensis*) (Kennedy *et al.*, 2013), Douglas fir (*Pseudotsuga menziesii*), and loblolly pine (Lachenbruch *et al.*, 2010; Shmulsky *et al.*, 2006). Portable acoustic tools have been developed for standing trees, which are not only non-destructive but also quicker to use and (hence) cheaper than conventional options (Matheson *et al.*, 2008). However, acoustic measurements may only partially correlate with stiffness and a better method to incorporate acoustic data with wood density measurements may improve predictions of the stiffness of standing trees. Thus, we studied the effectiveness of predicting the MOE of standing trees using Pilodyn and acoustic measurements (Chen *et al.* 2015).

1.4 Fibre length measurement

Large scale measurements of wood properties with sufficient accuracy and cost-efficiency are essential for assessing effects of silvicultural treatments, analysing wood variability, and genetically improving wood quality traits. Such techniques are available for assessing wood density, chemical composition, MFA, and mechanical properties of disc samples collected from felled trees, and increment cores from standing trees (Bergsten *et al.*, 2001; Chan *et al.*, 2010; Evans & Elic, 2001; Franceschini *et al.*, 2012; Jaakkola *et al.*, 2007; Schimleck & Evans, 2002). These are all important wood trait that influence properties of pulp, paper, and sawn products and thus are target for genetic tree improvements. Another is FL (Ivkovich *et al.*, 2002; Kibblewhite, 1999; Ververis *et al.*, 2004; Zobel & van Buijtenen, 1989), but measuring FL in conifers with fibres longer than 2 mm (Ilvessalo-Pfäffli, 1995) is problematic if increment cores are used for two reasons: long fibres are more likely to be cut (Mörling *et al.*, 2003) and the greater probability of sampling long fibres introduces sampling bias (Svensson *et al.*, 2007). Fibre cutting is negligible when 5-8 cm thick discs are used (Dutilleul *et al.*, 1998; Hannrup et al., 2004; Lundqvist, 2002; Lundqvist *et al.*, 2002; Lundqvist *et al.*, 2003; Molteberg & Høibø, 2006; Molteberg & Høibø, 2007), but felling of trees is not practical for large-scale studies since it is laborious, time-consuming, destructive and expensive. Hart and Hafley (1967) advocated trimming the outer sides of cores along the fibre direction to minimize the proportion of cut fibres, and measuring only uncut fibres to reduce the bias. However, this approach is also time-consuming, requires classification of cut and uncut fibres, and fibres longer than the core diameter cannot be observed. Therefore, a new method to reduce or correct the bias arising from cut fibres is desirable for measuring or estimating FL as accurately as possible. Such a new method was developed in the study reported in Paper IV. The biases in observed populations of fibres (and other cells) in an increment core are illustrated in Figure 4.

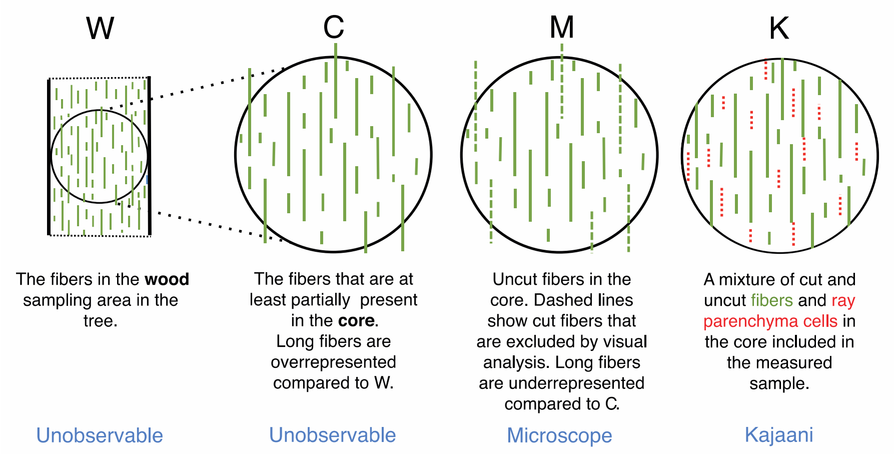


Figure 4. Illustration of four populations of fibres in the same wood core measured by a Kajaani FiberLab 3.5 instrument (Kajaani population, K) or microscopically (Microscope population, M). The two unobservable populations are the fibres in the wood-sampling part of the tree (wood population, W) and those that are at least partially present in the core (core population, C). The wood core is represented as a circle. Fibres and ray parenchyma cells included in each population are marked by solid green lines and red dots, respectively. The variables of interest are the fibre length distribution and mean length of fibres in an increment core taken from a randomly chosen position in the sampling part (W population).

1.5 Spatial analysis to increase accuracy of breeding value predictions

Due to the ability of spatial analysis to capture the continuous variation within blocks (patches) and global trends (gradients) across whole trials it has become very popular in agricultural and forestry field trials (Anekonda & Libby, 1996; Brownie & Gumpertz, 1997; Costa e Silva *et al.*, 2001; Cullis & Gleeson, 1989; Cullis & Gleeson, 1991; Cullis *et al.*, 1998; Dutkowski, 2005; Dutkowski *et al.*, 2006; Fox *et al.*, 2007b; Fox *et al.*, 2007c; Gilmour *et al.*, 1997; Qiao *et al.*, 2000; Yang *et al.*, 2004; Ye & Jayawickrama, 2008). In forestry, several spatial analysis methods have been introduced, such as post-blocking (Dutkowski *et al.*, 2002; Ericsson, 1999; Ericsson, 1997), nearest neighbour adjustment (Anekonda & Libby, 1996; Joyce *et al.*, 2002; Wright, 1978), and kriging (Hamann *et al.*, 2002; Zas, 2006). However, the most common method used is the experimental design features plus a spatial component in the form of separable first-order two dimensional autoregressive residuals, as recommended by Gilmour *et al.* (1997). This approach was used in the spatial analysis of variation in a large collection of Swedish Norway spruce field trials, as reported in Papers V and summarized in this thesis.

1.6 Dissecting genotype by environment interactions using factor analytic method

There are many traditional ways to analyse and detect patterns of G×E interactions, including analysis of variance (ANOVA), principal component analysis (PCA), and linear regression (Freeman, 1973). However, these methods are not always adequate to dissect a complex interaction structure (Zobel *et al.*, 1988). ANOVA can only test the significance of G×E interaction and the relative size of G×E interaction variance to genetic variance; it cannot provide any insight about its patterns. PCA can only assess the multiplicative effects of G×E interaction. Linear regression combines additive and multiplicative components. Various stability parameters can also be estimated from such regression to examine the stability of genotypes/families and test sites to infer causes of the interactions (McKeand *et al.*, 2003; Wu & Ying, 1998; Finlay & Wilkinson, 1963). For multiple-site progeny trials in forestry, among-site type-B genetic correlations have usually been estimated using a mixed linear model (Baltunis *et al.*, 2010). Since the 1980s, Singular Value Decomposition (SVD) has been employed to describe G×E interaction patterns (Gauch, 1992), initially in agronomic crops and later in forestry, using Additive Main effects and Multiplicative Interaction (AMMI) models. Recently, factorial regression using a mixed model approach (Factor analytic, FA) has been introduced to explore G×E patterns in crops in multiple environmental trials to relate underlying factors to causes of G×E interactions (Burgueño *et al*., 2008; Fox *et al*., 2007a; Mathews *et al*., 2007; Piepho, 1998; Smith *et al*., 2001; Smith *et al*., 2015). Besides linear and non-linear fixed and mixed parametric modelling approaches to decompose G×E interactions, there are also non-parametric methods to analyse G×E interaction, such as Multivariate Regression Tree (MRT) analysis (Hamann *et al*., 2011). For index selection with linear combination of many traits, G×E pattern for index is a function of relative importance of each traits (weights) and traits themselves (Namkoong, 1985).

In forestry, multiple regression and response surfaces are also commonly used to detect relationships between variation in populations and environmental gradients for inferring adaptive variation related to non-linear G×E (Campbell & Sorensen, 1978; Rehfeldt, 1983; Wang *et al*., 2010). In the studies underlying this thesis, G × E interaction patterns in the focal Swedish Norway spruce populations, and possible causes of the patterns, were explored using factor analytic method.

2 Objectives

The objectives of the studies this thesis is based upon were to accurately estimate genetic parameters and breeding values for growth and wood quality traits of Norway spruce in Sweden by: developing and applying better methods for measuring solid wood and fibre traits; using spatial analysis and factor analytic methods; and evaluating effects of incorporating wood quality traits into the Norway spruce breeding program. The following questions were specifically addressed:

1) What are the most reliable non-destructive methods to estimate wood stiffness and FL of standing trees for selective breeding purposes (Papers II and IV)?
2) How large is the heritability of wood quality traits important for solid wood, and pulp and paper products, and what are their genetic relationships with growth traits (Papers I and III)?
3) How can we incorporate solid wood quality traits and fibre properties into Norway spruce selective breeding programs, and how much gain will be obtained under different selection scenarios (Paper III)?
4) How much can the accuracy of breeding values for various types of traits be improved using spatial analysis (Paper V)?
5) What are G×E patterns for Norway spruce height in southern and central Sweden, and can we both select trees with the highest breeding values and obtain stable performance across-sites (Paper VI)?

3 Materials and Methods

3.1 Materials and field trials

To estimate genetic parameters for wood quality traits (such as wood density, MOE, and MFA) addressed in Paper I and fibre traits (RFW, TFW, FC, FWT, and FL) addressed in Paper III, of material in two progeny trials (designated F1146 and F1147; Chen *et al*. 2014), 524 half-sib families were selected. Two increment cores (12 mm) were taken using a boring machine at 1.3 m height from each of about 6000 trees in the two trials. One of each pair of cores was used to prepare a strip (Figure 5) to analyse using a SilviScan instrument, while the other was used to measure FL at cambial age 8-11 years using a Kajaani Fiber Lab 3.5 in Umeå (Papers III and IV). Pilodyn and Hitman instruments were used to measure Pilodyn penetration and acoustic velocity in the same ca. 6000 standing trees. The data were used in combination with SilviScan data in Paper II. For spatial analysis and estimation of G×E interaction in tree height (reported in Papers V and VI, respectively) 145 Norway spruce trials across Sweden and 20 half-sib trials with strong connections to parents in southern and central Sweden were used. The locations of all these Norway spruce trials were presented in Figure 6.

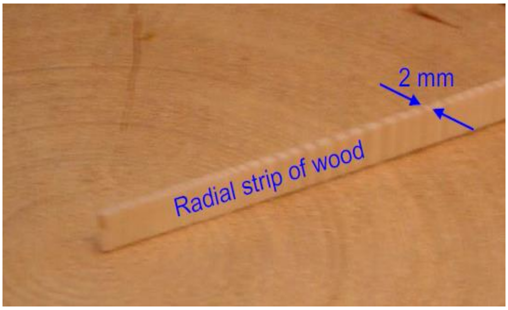


Figure 5. Illustration of the type of sample analysed with the SilviScan instrument (Sven-Olof)

Figure 6. Locations of all Norway spruce (*Picea abies* L. Karst) trials in this thesis.

Pilodyn penetration depth of the standing trees was measured using a Pilodyn 6J with a 2.0 mm diameter pin, without removing bark, while acoustic velocity was measured using a Hitman ST300 tool. Combined $\mathrm{MOE}_{(\mathrm{AV}^2+\mathrm{Pilo})}$ was calculated from pilodyn penetration (Pilo) and Hitman acoustic velocity (AV) measurements using the following equation:

$$\mathrm{MOE}_{(\mathrm{AV}^2+\mathrm{Pilo})} = (1/\mathrm{Pilo}) * 10000 * \mathrm{AV}^2$$

Annual rings 8-11 were cut from 2973 increment cores and FL was measured using a Kajaani FiberLab 3.5 instrument. In addition, FL was measured in eight fast-growing and eight slow-growing trees by both the Kajaani FiberLab 3.5 and microscopic observation for comparison (Paper IV), and three other trees from the same progeny trial were analysed to assess the precision of mean FL estimates based on Kajaani FiberLab measurements.

Based on Kajaani FiberLab measurements four types of FL averages were calculated: the arithmetic mean length (Ln), length-weighted mean length (Ll), squared length-weighted mean length (Ll^2), and expectation–maximization mean length ($\mathrm{L_wEM}$).

3.2 Statistical analysis

3.2.1 General model

Linear mixed models were used for univariate and multivariate analyses. In general form, the univariate model equation is:

$$y = Xb + Zu + e$$

with $E(y) = Xb$ and $Var(y) = V = ZGZ' + R$; where y is the vector of each individual tree observation, b is the vector of the fixed effect, u is the vector of random effect and e is the vector of residuals. X and Z are incidence matrices of fixed effect (b) and random effect (u), respectively. The u and e are assumed to be independent and normal distributions such as u~$(0, \sigma^2 A)$, e~$(0, \sigma_e^2)$, where A is the numerator relationship matrix.

Estimates of fixed and random effects are obtained by solving the linear mixed model equations (Henderson, 1984):

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where R is the variance-covariance matrix of the residuals and G is the direct sum of each of the random effects. Where residuals are assumed to be independent, R is defined as σ_e^2I.

In the studies reported in Papers I, II, and IV, bivariate models were used to estimate genetic correlation between considered traits, age-age correlations, and type-B genetic correlations (genetic correlations for the same traits in different sites).

Multivariate analysis was used in the multivariate selection described in Paper IV.

3.2.2 Spatial analysis

In Papers V and VI, spatial analysis was used to dissect the variation in field trials. Generally, including design and spatial effects gives the best results according to ASReml log-likelihood ratio tests (Dutkowski *et al.*, 2002).

For linear mixed models, if residuals included spatially dependent (ξ) and independent (η) residuals, we used a covariance structure to express ξ assuming separable first-order autoregressive processes in rows and columns, for which the R matrix is:

$$\mathrm{R} = \sigma_\xi^2 \left[\mathrm{AR1}(\mathrm{p}_{\mathrm{col}}) \otimes \mathrm{AR1}(\mathrm{p}_{\mathrm{row}})\right] + \sigma_\eta^2 \mathrm{I}$$

where σ_ξ^2 is the spatial residual variance, σ_η^2 is the independent residual variance (parameters estimated by Restricted Maximum Likelihood, REML), I is an identity matrix, $\otimes$ is direct products for two matrices and AR1(p) represents a first-order autoregressive correlation matrix for columns and rows.

When a variogram of residual showed an un-flat platform, spline, polynomial, and linear functions were used to make it stationary. Edge effects were also used when edges of row or column trees grew rapidly.

3.2.3 Factor analytic

In the study described in paper VI, a factor analytic model was used to estimate additive across-site genetic effects. The additive genetic effect, $u_{a_{p_{ij}}}$ for the ith parent at site j can be viewed as arising from a multiplicative model:

$$u_{a_{p_{ij}}} = \lambda_{a_{1j}} f_{a_{1i}} + \lambda_{a_{2j}} f_{a_{2i}} + \cdots + \lambda_{a_{kj}} f_{a_{ki}} + \delta_{a_{ij}}$$

where the equation includes a sum of k multiplicative terms. Each term is the product of a genetic effect ($f_{a_{ri}}$), which is known as a factor score, and an environment effect ($\lambda_{a_{rj}}$), which is known as a site loading. This model, therefore, represents a regression of G×E effects on the site loadings (unknown covariates) with different slopes (scores) for each parents. It can be written in vector notation as:

$$\mathrm{u}_a = (\mathrm{I}_m \otimes \Lambda_a) f_a + \delta_a$$

where $\Lambda_a$is the $t \times k$ matrix of site loadings, f_a is the $mk \times 1$vector of additive genetic scores (slopes) and $\delta_a$is the $mt \times 1$vector of lack of fit or genetic regression residuals.

f_{a} and δ_{a} are assumed to be independent and have multivariate Gaussian distributions with zero means and variance matrices given by:

$$var(f_a) = A \otimes \mathrm{I}_k \text{ and } \mathrm{var}(\delta_a) = A \otimes \Psi_a$$

where Ψ_a is a $t \times t$ diagonal matrix with a variance for each site. These assumptions lead to $\mathrm{var}(\mathrm{u}_a) = A \otimes (\Lambda_a \Lambda_a^T + \Psi_a)$.

After model fitting, the site loading and score of each parent for each of k factors should be rotated as follows (Cullis *et al.*, 2010):

$$\Lambda_a^* = \Lambda S$$

where S is the singular value decomposition of Λ.

3.2.4 Index selection

Multivariate linear mixed models were used to estimate phenotype and genetic variance-covariance matrices. Different selection scenarios were considered in paper I and paper IV. In the analysis presented in Paper I restricted index selection was used to select for growth, with no change in wood quality traits. In the analysis presented in Paper IV both economic weights and restricted indices were used to evaluate seven selection scenarios, including selection to combine growth and wood stiffness and their effects on fibre properties.

The index coefficients were obtained from:

$$\mathrm{b} = \mathrm{P}^{-1}\mathrm{Ga}$$

where P is the phenotypic variance-covariance matrix for selection traits, G is the additive genetic variance-covariance matrix between selection traits and objective traits, and a is the vector of economic weights for each of the objective traits (Mrode & Thompson, 2005).

For a restricted selection index this equation could be modified as:

$$\mathrm{b}^{*} = \begin{bmatrix} \mathrm{P}^{*} & \mathrm{G}^{*} \\ \mathrm{G}^{*\prime} & 0 \end{bmatrix} \begin{bmatrix} \mathrm{G}^{\mathrm{x}} \\ 0 \end{bmatrix} \mathrm{v}$$

where P* is the phenotypic variance-covariance matrix for selection traits, excluding the restricted trait, G* is the additive genetic variance-covariance matrix between selection traits and traits excluding restricted traits, G^{X} is the additive genetic variance-covariance matrix between selection traits excluding restricted traits, v is the vector of economic weights of all traits, 0 is the zero vector (Cunningham *et al.*, 1970). Genetic gain was calculated using mass selection for a single trait. Profitability was calculated using diameter and MOE from:

$$\mathrm{Pr} = 1\mathrm{G}_{\mathrm{d}} + 10\mathrm{G}_{\mathrm{M}}$$

where Pr is the Profitability, G_{d} is the genetic gain of diameter (mm), G_{M} is the genetic gain of MOE (GPa). The coefficients of 1 and 10 for G_{d} and G_{M} are the economic weights, based on the published data (Ivković *et al.*, 2006). We also estimated genetic gain and profitability with economic weights of MOE ranging from 1 to 25 relative to the economic weight for diameter (1).

3.2.5 Statistical software

All the statistical analyses were done using ASReml 3.0 (Gilmour *et al.*, 2009) and ASReml-R package in R (Butler *et al.*, 2009).

4 Results and Discussion

4.1 Method for predicting wood stiffness

The accuracy of predictions of the stiffness of wood in standing trees based on Pilodyn (Pilo) and Hitman acoustic velocity measurements was addressed in Paper II, using SilviScan measurements of MOE as benchmarks, following previous evaluations (Evans & Elic, 2001; Raymond *et al.*, 2007).

The squared acoustic velocity (AV^2) obtained from Hitman measurements was found to be highly genetically correlated with MFA (-0.93), but only moderately genetically correlated with wood density (0.47). Pilodyn measurements had a high genetic correlation with wood density (0.96), but relatively low genetic correlation with MFA (0.30). These findings indicate that Pilodyn measurements could be considered robust indirect measurements of wood density in Norway spruce. Similar results have been previously reported for several species, including Norway spruce, radiata pine and *Eucalyptus nitens* (Costa e Silva *et al.*, 2000; Cown, 1978; Greaves *et al.*, 1996). We also found that the combination of AV^2 and Pilo measurements had almost perfect genetic correlation (0.99) with the benchmark SilviScan MOE measurements.

4.1.1 Efficiency of selection using Pilodyn and Hitman measurements of wood quality traits

The efficiency of indirect selection based on Pilodyn and Hitman measurements of standing trees compared with benchmark wood quality traits (wood density, MFA, and MOE) was addressed in Paper II. Selection based on AV^2 had 94% efficiency for MFA, and selection based on Pilodyn measurements had high efficiency (80%) for wood density, relative to the respective benchmarks. Indirect selection based on predicted MOE of standing trees using the AV^2+Pilo indicator had 92% efficiency for MOE, relative to the benchmark, much higher than efficiencies obtained using either acoustic velocity or Pilodyn measurements alone (60 and 78%, respectively).

4.2 Method for accurately determining fibre length

We compared distributions of microscopic measurements of the length of uncut fibres in 16 trees with the distribution of Kajaani measurements of the same samples. All intact fibres we found were longer than 0.67 mm, indicating that all shorter records in Kajaani datasets would be measurements of cut fibres or ray parenchyma cells. In addition, we found no substantial difference in FL distributions between the M and W populations illustrated in Figure 7.

We also found that ranking of the 16 trees according to mean FL (mFL) depended on the FL measurement and calculation methods used. Spearman's rank correlations between benchmark microscopic measurements (L_wM) and 4 types of Kajaani-based estimates (L_wEM, $L1^2$, L1 and Ln) were 0.92, 0.76, 0.71 and 0.37, respectively, indicating that ranking using L_wEM estimates is optimal.

The precision of each of the Kajaani-based mFL estimates could be controlled by analysing several subsamples from the same core by optical fibre analysers, then using the average of the subsample mFL estimates as the final one. To gain insight into the variation, we computed mFL estimates based on Kajaani data for 20 subsamples of increment cores from three trees. Repeated measurements showed that Kajaani mean length estimates for three subsamples provided a 95% confidence interval of around 0.06 mm.

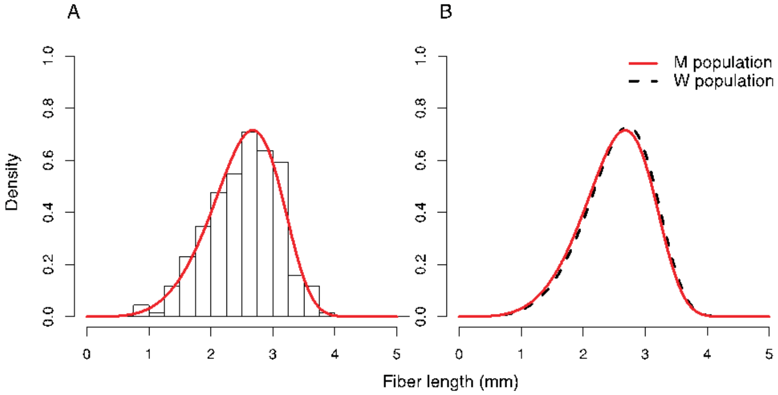


Figure 7: (A) Histogram of microscopically determined lengths of 277 randomly selected uncut fibres from a 12-mm increment core sample, and corresponding ML-estimated density function of uncut fibre lengths in the core. (B) Estimated length distributions of uncut fibres in the core ('M' population, microscopically observed) and fibre length distribution in the wood sampling part ('W' population) estimated using the EM algorithm from Kajaani measurements of the same core (cambial age, 8-11 years).

We developed a method based on expectation–maximization (EM) for estimating FL distributions, which has several theoretical advantages, as presented and discussed in Paper III. The accuracy of estimates of genetic parameters using this method is further presented here, using the standard errors of estimated genetic parameters. The new EM method to calculate FL consistently gave lowest standard errors than other approaches (Table 1).

Table 1. Numbers of observations (N) and narrow-sense heritabilities (h_i^2) for mean fibre length estimated by indicated Kajaani-based methods, and genetic correlations between the fibre length estimates and mean ring width (MRW), density, radial fibre width (RFW), tangential fibre width (TFW), fibre cell wall thickness (CWT) and fibre coarseness (FC) measurements.

	N	h_i^2	MRW	Density	RFW	TFW	CWT
Ln	3108	0.44 (0.12)	0.09 (0.21)	-0.24 (0.15)	0.09 (0.15)	-0.19 (0.14)	-0.28 (0.15)
Ll	3108	0.50 (0.13)	-0.07 (0.18)	0.04 (0.13)	0.15 (0.14)	0.12 (0.15)	0.13 (0.13)
Ll^2	3108	0.50 (0.13)	-0.09 (0.17)	0.03 (0.12)	0.12 (0.12)	0.26 (0.13)	0.13 (0.12)
L$_w$EM	3108	0.41 (0.12)	-0.14 (0.17)	0.15 (0.12)	0.11 (0.12)	0.10 (0.14)	0.24 (0.12)

Note: Ln, arithmetic mean fibre length; Ll, length-weighted mean fibre length; Ll^2, squared length-weighted mean fibre length; L$_W$(EM), estimated mean fibre length in the wood sampling area computed by the EM-algorithm.

4.3 Coefficients of variation for growth and wood quality traits

Mean values, coefficients of variation, and narrow-sense heritabilities for growth and wood quality traits determined from SilviScan, Pilodyn and Hitman data are shown in Table 2. Generally, coefficients of additive (CV_a) and phenotypic (CV_p) variation were higher for growth traits than for solid wood quality traits, except for SilviScan-based MFA. In addition, higher CV_a and CV_p were found for solid wood traits than for fibre traits (e.g. RFW, TFW, FWT, FC, and FL). Park *et al.* (2012) found similar patterns in white spruce, but Hong *et al.* (2014) found that solid wood traits have higher CV_a and CV_p than growth traits (except volume) in Scots pine.

CV_a and CV_p of DBH decreased between tree ages 12 and 21 years, in accordance with age-related trends in height of Norway spruce trees detected by Kroon *et al.* (2011) using available data from all Swedish trials. Pilodyn and Hitman measurements of standing trees provided similar CV_a and CV_p values to those obtained from SilviScan measurements of increment cores for all considered wood quality traits (e.g. density and MOE), except MFA.

4.4 Inheritance of wood quality traits

The heritability of DBH reported in Paper I is slightly higher than previously recorded (Gräns *et al.*, 2009; Hannrup *et al.*, 2004; Steffenrem *et al.*, 2009) because of the truncated selection (only the relatively large healthy trees within each family were considered), as also found when using the data for all trees in the same trial (Paper II).

Generally, wood quality traits have higher heritability than growth traits in conifer species (Hong *et al.*, 2014; Wu *et al.*, 2008). We found the same pattern, as shown in Table 2, except for MFA (which had a low heritability value of 0.15). The deviation in MFA was probably due to compression wood or other unknown factors causing changes in MFA with age in the outer parts of some wood sections, as shown in Figure 8. In normal samples MFA continuously decreased then stabilized in the outer rings (Figure 8a), but in about 20% trees it increased in this zone, outwards from ca. cambial age 7 years (Figure 8b). The abnormal curves in these samples were responsible for the low heritability of MFA, which substantially increased if samples with such profiles were excluded from the analyses.

Table 2. Numbers of observations (N), mean values, coefficients of additive (CV_a) and phenotypic (CV_p) variation and narrow-sense heritabilities (h_i^2) for wood quality traits of Norway spruce obtained using joint-site data (parameters presented in Papers I, II, and III).

Triat	N	Mean	CV_a (%)	CV_p (%)	h_i^2
Growth traits					
DBH_{12} (mm)	25498	57.7	15.45	31.62	0.24 (0.02)
DBH_{21} (mm)	21425	102.8	11.91	28.10	0.18 (0.02)
Ht_7 (cm)	26213	222.4	14.93	29.25	0.26 (0.02)
Indirect wood traits					
$Pilo_{22}$ (mm)	5712	21.4	6.97	11.93	0.34 (0.05)
AV_{24}^2 (km s^{-1})^2	5557	17.54	5.04	12.95	0.15 (0.05)
$MOE_{(AV^2+Pilo)}$ (GPa)	5557	8.35	9.63	18.32	0.28 (0.05)
Benchmark SilviScan wood traits					
$Density_{21}$ (Kg.m^{-1})	5498	429.8	6.11	8.67	0.50 (0.06)
MFA_{21} (°)	5498	14.16	11.63	30.24	0.15 (0.04)
MOE_{21} (GPa)	5498	12.28	9.89	17.27	0.33 (0.05)
RFW_{21} (µm)	5498	29.43	4.07	5.90	0.48 (0.06)
TFW_{21} (µm)	5498	27.45	2.87	4.95	0.34 (0.05)
FWT_{21} (µm)	5498	2.15	5.54	8.29	0.45 (0.06)
FC_{21} (µg/m)	5498	330.60	5.15	8.88	0.34 (0.05)
FL_{8-11} (mm)	3108	2.45	5.32	8.31	0.41 (0.08)

RFW, radial fibre width; TFW, tangential fibre width; FWT, fibre wall thickness; FC, fibre coarseness; FL, mean fibre length estimated by the new method presented in Paper III.

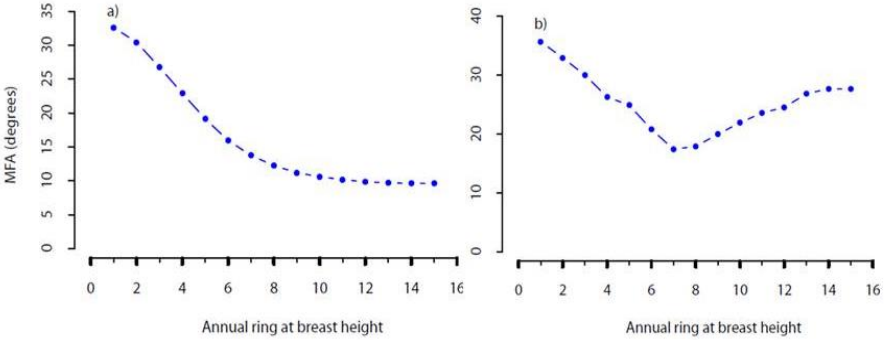


Figure 8. a) Normal MFA curve, declining with increases in cambial age then stabilising; b) abnormal MFA curve, declining with increases in cambial age until ring 7 then rising.

4.5 Genetic correlations among growth, solid wood, and fibre traits

Adverse genetic correlations among tree diameter and wood quality traits, including solid wood and fibre traits, are commonly found in conifer species, but the strengths of phenotypic and genetic correlations across whole increment cores and parts of cores vary in different species (Hong *et al.*, 2015; Lenz *et al.*, 2010; Lenz *et al.*, 2011; Zobel & Jett, 1995). We detected a number of adverse genetic correlations, as described in Papers I and IV, which are consistent with previously reported correlations in Scots pine (Fries, 2012; Hong *et al.*, 2014) and white spruce (Ivkovich *et al.*, 2002; Park *et al.*, 2012), and radiata pine (Wu *et al.*, 2008). Our findings regarding these correlations are summarized here.

We found that solid wood quality traits had stronger unfavourable genetic correlations (positive or negative) than fibre dimensions with DBH (0.54-0.75 and 0.11-0.49, respectively). Such strongly unfavourable correlations pose major challenges for improving solid wood quality traits in tree breeding programs. Several authors have previously reported similar patterns in Norway spruce reported (Gräns *et al.*, 2009; Hannrup *et al.*, 2004), but no previous studies have evaluated possible solutions to the challenges so thoroughly.

MOE is known to be correlated with MFA and wood density (Wu *et al.*, 2007), but we found that SilviScan-derived MOE estimates had slightly stronger genetic correlation with SilviScan-derived wood density measurements (0.87) than with MFA (-0.75) in Norway spruce. However, slightly stronger negative genetic correlations between MFA and MOE have also been reported in earlier studies on conifer species (Baltunis *et al.*, 2007; Hong *et al.*, 2014; Lenz *et al.*, 2011) and *E. delegatensis* (Evans & Elic, 2001). However, Lenz *et al.* (2011) reported that the genetic correlation between MOE and wood density was extremely weak in juvenile wood of white spruce.

Correlation estimates between radial growth and fibre traits were low to moderate, being strongest for FWT (-0.51) and RFW (0.49), so trees with high volume growth tend to have wide fibres with thin walls, and thus low wood density (-0.61). FC also tends to decrease with increases in volume (-0.24), as FWT normally decreases more (proportionally) than fibre width. Density also showed moderate genetic correlation with FC (0.58). All these correlations were consistent with expectations and stable across rings, as shown in Paper IV. Assuming that the density of fibre walls is constant, wood density should increase if FWT and FC increase, and decrease if RFW and TFW increase.

Nyakuengama *et al*. (1997) reported that FWT is also the main determinant of wood density in radiata pine, in line with the stronger correlation between FWT and density than between FWT and density we found. Similar patterns have been found in Scots pine (Hong *et al*. 2014) and white spruce (Lenz *et al*. 2010). The moderate negative correlation between TFW and density we observed in Norway spruce is also consistent with previous findings by Hannrup *et al*. (2004). However, Hong *et al*. (2014) reported a negligible positive genetic correlation between density and TFW in Scots pine, while Lenz *et al*. (2010) found that RFW and TFW had moderate negative and positive genetic correlations, respectively, with density.

The correlations of FL with other fibre dimensions were weak, but we detected a moderate correlation with FC (0.48). Thus, the length of the fibres is not strongly correlated with wood density and radial growth, and may not be substantially affected by selective breeding for diameter. However, our findings indicate that selection to increase diameter will reduce wood density and FWT.

4.6 Age-age correlation and early selection efficiency for wood quality traits

We found that age-age genetic correlations from early rings to reference ring 15 are very high for all wood quality traits in Norway spruce (Papers I and III), reaching 0.9 at ring four for DBH, density, MFA, MOE, and RFW; ring six for TFW and FWT; and ring seven for FC. Together with the high heritability of the wood quality traits, the high age-age genetic correlations indicate that early selection for wood quality traits in the Norway spruce breeding program would be highly feasible. More specifically, we found that selection at ring six would be 80% as effective as selection at reference ring 15, although selection efficiency would still gradually improve with further increases in ring age. Similar patterns have been found in white spruce (Lenz *et al*., 2011). Early selection efficiency for MFA at ring four would be as efficient as selection at the reference ring 15. However, due to the lower heritability of MFA after ring six, we detected a decline in early selection efficiency with increasing age after ring six, suggesting selection at this ring age would be most efficient.

We found that the optimal early selection age for MOE was seven years, similar to the reported optimal age for radiata pine (Li & Wu, 2005; Wu *et al*., 2007), but substantially younger than the corresponding age (later than ring 16) reported for white spruce (Lenz *et al*., 2011).

Early selection efficiency for RFW reached 1 from ring six, earlier than in white spruce according to Lenz *et al*. (2011). Similarly, early selection for FWT reached 1 at ring 10, while in white spruce selection efficiency gradually improves to the reference ring age 16 (Lenz *et al*., 2011). Our results indicate that early selection at rings five, ten, eight and eight will provide at least 90% selection efficiency for RFW, TFW, FWT, and FC, respectively.

4.7 Spatial analysis of spruce trials

Spatial modelling has been widely used to reduce environmental variation and improve the accuracy of estimated breeding values (EBVs) in Sweden. For these reasons we applied spatial analysis to a large data set (covering 464 variables associated with nine types of traits of Norway spruce in 145 trials across Sweden). The methods and results are presented in detail in Paper V, and summarised here.

Including spatial components significantly improved the log likelihood of models for 392 (88%) of the 464 variables. The largest improvements were for growth and wood quality traits: there were significant improvements for 98% of diameter, 99% of height, and 100% of wood quality variables, and proportions of substantial improvements (e.g. >50 change in log likelihood, ΔLL) were also highest for these variables. Improvements were fewest and weakest for multiple stem, insect damage and bud burst variables, while spatial elements improved branch, stem straightness, and frost resistance models moderately.

Large trials, where block variance explained a large amount of variation, tended to provide the largest improvements in log likelihood. Block variance accounted for < 10% of the total variance for 282 variables (65%), and data for most non-significant variables (10.3%) had been mainly collected from small trials where the block variance component was < 10%.

Generally, spatial analysis reduced all mean block variances (σ_B^2) for all nine types of traits, but the reduction varied substantially, from 45% for bud burst to 86.1% for stem diameter, with a mean reduction of 66.2%. Spatial analysis reduced block variance more than 80% for diameter, height and stem traits. For example, it decreased the average block variance (σ_B^2) for diameter from 13.4 % to 2.2 %. However, it slightly increased block variances for some branch, diameter, frost resistance and height traits, for example two (3.1%) branch variables and one (4.8%) frost variable.

Spatial analysis had inconsistent effects on additive genetic variance (σ_A^2), in general accordance with other reports (Dutkowski *et al.*, 2006; Dutkowski *et al.*, 2002; Ye & Jayawickrama, 2008), although some studies have found it increased σ_A^2 (Anekonda & Libby, 1996; Ball *et al.*, 1993; Hamann *et al.*, 2002; Kusnandar & Galwey, 2000). Magnussen (1993, 1994) found that simulation-derived data increased σ_A^2. Dutkowski *et al*. (2002) considered that consistent increase of additive variances in the simulation study may be due to no independent error term in model.

Fitting to a spatial model increased heritability estimates for all nine types of traits, by 16.7% on average, and for 94.7% of the variables (ranging from 83% of insect damage variables to 100% of variables related to form, multiple stems, bud burst, and wood quality traits). The largest average improvements were for diameter and height (26.0% and 34.2%, respectively). Spatial modelling also reportedly increases heritability estimates slightly more for height than for diameter in Douglas fir (Ye and Jayawickrama, 2008). Both base and spatial models indicated that the heritability of bud burst variables is substantial (0.78 and 0.81, respectively).

Spatial modelling increased the average accuracy of breeding values for six types of traits (branch, diameter, insect, height, and wood quality) but decreased it for frost, multiple stem and bud burst traits. However, the changes were small; the largest increases (for insect damage, tree diameter and height traits) being 4.96, 1.76, and 1.56%, respectively. The accuracy of breeding value predictions for tree diameter, height, and wood properties was higher for 86.9, 73.53, and 75% of cases, respectively, in spatial than in base models. Similarly, increases in the accuracy of breeding value predictions for progeny were highest for tree diameter and height (3.60 % and 3.44%, in 95.24% and 81.76% of cases, respectively).

For both parents and offspring, Spearman´s rank correlations between breeding values predicted by base and spatial models were very high; > 0.94 for all cases except those for wood quality of offspring (although they were still high, e.g. 0.89).

Mean increases in estimated genetic gain for the nine trait types ranged from 0% to 6.24% for parents and 0.43% to 3.66% for offspring. Spatial models provided the largest increases, relative to base models, in estimated gain in tree diameter, height, and wood properties (1.91%, 4.24%, and 6.24% for parents and 3.56%, 4.24%, and 3.66% for progeny, respectively).

Spatial first-order autocorrelations were high for most examined variables. The average autocorrelations among columns and rows were 0.76 and 0.79, respectively. Autocorrelations (among columns and rows) were higher (>0.80) for diameter, height, and wood quality traits, possibly because these traits had been more affected by continuous global or local variation in microsite factors such as soil nutrient contents, soil depth and waterlogging.

We found that autocorrelation coefficients for growth and branch traits were slightly positively correlated with tree age, possibly because trees in Swedish Norway spruce trials are still too small (most of them are younger than 15 years) to compete strongly, as competition is often manifested in negative autocorrelation coefficients (Costa e Silva *et al*., 2013; Magnussen, 1989; Reed & Burkhart, 1985). A summary by Fox *et al*. (2001) of several studies (Anekonda & Libby, 1996; Kuuluvainen *et al*., 1996; Magnussen, 1994; Magnussen & Yeatman, 1987) confirmed a hypothesis by Reed and Burkhart (1985) that before canopy closure stands usually exhibit positive spatial dependence, while competition following canopy closure may result in negative spatial dependence until senescence, when stands tend to show a positive spatial dependence again. We only detected a (small) negative autocorrelation for one growth variable in one direction, indicating that there may be little competition up to the age of genetic parameter estimates and early selection in the Swedish Norway spruce breeding program. Ye and Jayawickrama (2008) considered that autocorrelation is likely to be relatively weak but still positive when both strong spatial association and competition are present. We found < 0.5 autocorrelation coefficients for three variables in one direction for DBH at ages of 12, 16 and 20 years. Further analysis of indirect genetic effects using the competition model recommended by Costa e Silva *et al*. (2013) and Costa e Silva and Kerr (2013) may be warranted.

We found that models for nine variables (including height, diameter, branch angle, and frost variables) of materials in the progeny trials had non-significant independent residual errors. When modelling data from most forestry trials including both an independent and an autoregressive error is generally necessary (Costa e Silva *et al*., 2001; Dutkowski *et al*., 2002; Kusnandar & Galwey, 2000). If models are fitted without the independent error, the additive genetic variance could be substantially inflated and actual patterns of spatial variation could be obscured. However, in accordance with Dutkowski *et al*. (2006), we also found that in some cases there were no independent error variances in the forestry trials. In agricultural experiments, an extended model is recommended when non-significant independent error is observed (Gilmour *et al.*, 1997). Therefore, an extended model was used to examine the possible improvement it could provide for parental and offspring breeding values and selection gains in these nine variables. However, use of the extended model had very little impact on estimates of either breeding values or genetic gain.

4.8 Patterns of genotype by environment interaction in tree height

4.8.1 Genotype by environment interaction in wood quality

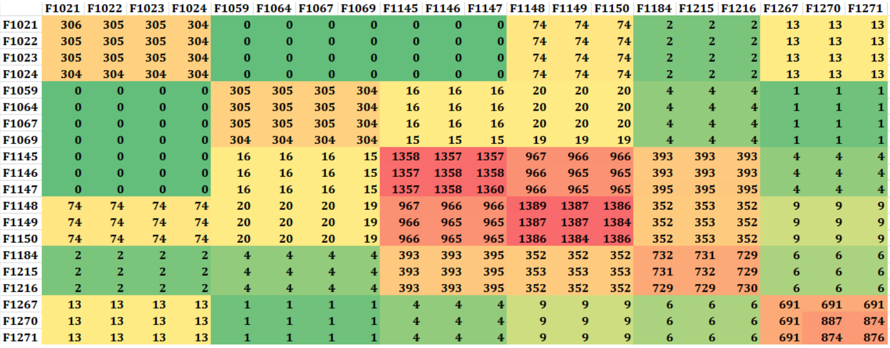
According to estimates based on data regarding two sites (F1146 and F1147) type B genetic correlations for solid wood quality and fibre traits were all > 0.74 (Papers I and III), indicating that G×E interaction might not be important for wood quality traits in Norway spruce, in accordance with analyses of other conifers (Apiolaza, 2012; Baltunis *et al.*, 2010; Gapare *et al.*, 2010). However, analysis of material in more sites covering broader parts of southern Sweden is warranted to examine regional G×E trends..

4.8.2 Genotype by environment interaction for growth traits

In accordance with general findings (Apiolaza, 2012; Cullis *et al.*, 2014; Ivković *et al.*, 2015), we found that G×E interaction was stronger for growth traits, such as DBH and tree height, than for wood quality traits (Papers I, II, III, and VI). The estimated type B genetic correlation for annual ring width was 0.45 (Paper I), and a mean (median) of 0.48 (0.58) for tree height was observed in 20 half-sib progeny trials located in southern and central Sweden (Paper VI).

4.8.3 Factor analytic to explore the GXE interaction for tree height

We explored G×E interaction patterns in tree height in southern and central Sweden by factor analytic model, as reported in Paper VI. It is very important to understand the genetic connectivity between trials before analysing such data (Cullis *et al.*, 2014). Therefore, the parental concurrence between trials is presented in Figure 9 as a heatmap. The diagonal elements of the matrix are numbers of female parents used in the trials and the off-diagonal elements are numbers of female parents in common among sites. Three sites (F1148, F1149, and F1150) had the best connection with all other sites, while four sites (F1021, F1022, F1023, and F1024) had no connections with seven other sites.



	F1021	F1022	F1023	F1024	F1059	F1064	F1067	F1069	F1145	F1146	F1147	F1148	F1149	F1150	F1184	F1215	F1216	F1267	F1270	F1271
F1021	306	305	305	304	0	0	0	0	0	0	0	74	74	74	2	2	2	13	13	13
F1022	305	305	305	304	0	0	0	0	0	0	0	74	74	74	2	2	2	13	13	13
F1023	305	305	305	304	0	0	0	0	0	0	0	74	74	74	2	2	2	13	13	13
F1024	304	304	304	304	0	0	0	0	0	0	0	74	74	74	2	2	2	13	13	13
F1059	0	0	0	0	305	305	305	304	16	16	16	20	20	20	4	4	4	1	1	1
F1064	0	0	0	0	305	305	305	304	16	16	16	20	20	20	4	4	4	1	1	1
F1067	0	0	0	0	305	305	305	304	16	16	16	20	20	20	4	4	4	1	1	1
F1069	0	0	0	0	304	304	304	304	15	15	15	19	19	19	4	4	4	1	1	1
F1145	0	0	0	0	16	16	16	15	1358	1357	1357	967	966	966	393	393	393	4	4	4
F1146	0	0	0	0	16	16	16	15	1357	1358	1358	966	965	965	393	393	393	4	4	4
F1147	0	0	0	0	16	16	16	15	1357	1358	1360	966	965	965	395	395	395	4	4	4
F1148	74	74	74	74	20	20	20	19	967	966	966	1389	1387	1386	352	353	352	9	9	9
F1149	74	74	74	74	20	20	20	19	966	965	965	1387	1387	1384	352	353	352	9	9	9
F1150	74	74	74	74	20	20	20	19	966	965	965	1386	1384	1386	352	353	352	9	9	9
F1184	2	2	2	2	4	4	4	4	393	393	395	352	352	352	732	731	729	6	6	6
F1215	2	2	2	2	4	4	4	4	393	393	395	353	353	353	731	732	729	6	6	6
F1216	2	2	2	2	4	4	4	4	393	393	395	352	352	352	729	729	730	6	6	6
F1267	13	13	13	13	1	1	1	1	4	4	4	9	9	9	6	6	6	691	691	691
F1270	13	13	13	13	1	1	1	1	4	4	4	9	9	9	6	6	6	691	887	874
F1271	13	13	13	13	1	1	1	1	4	4	4	9	9	9	6	6	6	691	874	876

Figure 9. Common female parents in each of 20 trails

In the final model (designated FA3) — selected according to results of an ASReml log-likelihood ratio test (REMLRT) and two Information Criteria (Bayesian and Akaike) — the first three factors explained 92.9% of the additive by site interaction variance. The rotated loadings for these factors accounted for 56.34, 23.45, and 13.31% of the additive genetic variance, respectively.

The site-site additive genetic correlation matrix for tree height (also obtained using the FA3 model) is represented by a heatmap with dendrograms added to the left and the top in Figure 10. Additive site-site correlations varied from -0.76 to 0.98 with a mean (median) of 0.48 (0.58). Three sites (F1267, F1270, and F1271) had particularly low additive site-site genetic correlations with other sites (Figure 10), and very low connection with all other sites. Excluding these three trials increased the mean (median) additive site-site correlation to 0.54 (0.65).

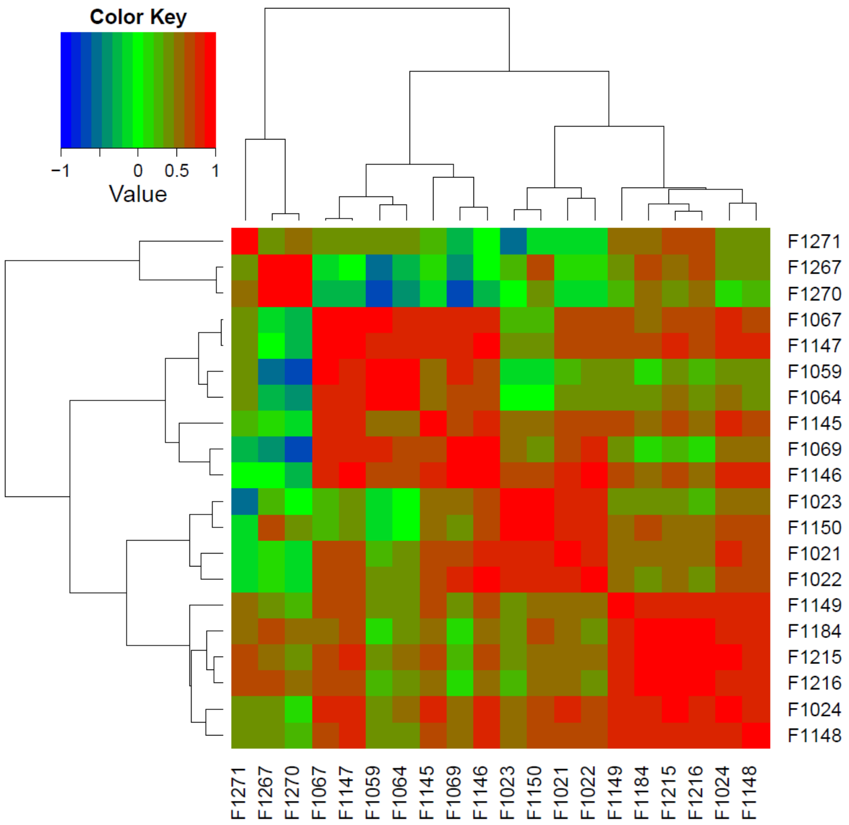


Figure 10. Heat map and dendrogram of cross-site additive genetic correlations for height.

The correlations between climate variables and the rotated site loadings for the three factors highlighted the importance of the climatic variables' contributions to the G×E interactions. Under the FA3 model, the three factors' site loadings are moderately to highly correlated to annual mean temperature (AMT) (0.41, 0.42, and -0.28), annual heat sum (AHT) (0.30, 0.33, and -0.20), mean daily temperature in May and June (MTMJ) (0.65, 0.44, and -0.46), and mean daily temperature in September and October (MTSO) (0.55, 0.27, and -0.50). The only geographical variable showing significant correlation with site loadings for all three factors was latitude (-0.45, -0.36, and 0.21). Therefore, the mean daily temperature in spring (May and June) and autumn (September and October) contributed most strongly to the G×E interaction in traits of Norway spruce trees in the trials.

4.9 Selection scenarios for wood quality traits

Several selection scenarios were considered in the studies (Papers I and III), with a constant selection intensity (i) of 2.67 (i.e., 1%). Selection based on diameter alone resulted in an increase of 19.0% in DBH, but unfavourable 4.9, 9.4, and 8.0% changes in wood density, MFA, and MOE, respectively (Paper I). A selection index imposing no change restrictions in wood density, MFA, and MOE would result in lower gains in diameter, of 16.4, 14.1, and 12.0%, respectively. No economic weights were used in the selection scenarios considered in Paper I.

In paper III, the economic weights for growth and MOE used in radiata pine were adopted in our scenario analyses for Norway spruce in order to study the effect of combined index selection using growth and wood stiffness on fiber traits. The results of seven selection scenarios were showed in Table 2. Selection based on DBH alone would incur a slight (negligible) decrease of fiber length (FL, 1.1%) and fiber wall thickness (FWT, 2.9%), but a large decrease of stiffness (MOE, 9.6%). Similarly, selection based on MOE alone would have a slight decrease of fiber size (RFW, 3.6% and TFW, 1.6%), but a large decrease of DBH (Diameter, 13.8%).

In subsequent analyses reported in Paper III, previously used economic weights for growth and MOE of radiata pine (Ivković et al., 2006) were applied to evaluate effects on fibre traits of selection based on combined growth and wood stiffness indices. The results of seven selection scenarios are shown in Table 3. Selection based on DBH alone (scenario A) would incur slight (negligible) decreases in FL (1.1%) and FWT (2.9%), but a large decrease in stiffness (MOE, 9.6%). Similarly, selection based on MOE alone (scenario B) would cause slight reductions in fibre size (3.6 and 1.6% reductions in RFW and TFW, respectively), but a large decrease in DBH (13.8%). Selection based on economically-weighted diameter and stiffness (scenario C) would result in different outcomes, e.g. a much smaller increase (10.5%) in diameter, very little change in FL, but small increases in MOE (0.2%) and fibre size (1.5 and 1.1% increases in RFW and TFW, respectively), with a major increase in overall profitability. Selection for diameter with a restriction of no change in FL (scenario D) would have a similar outcome to selection based on DBH alone, and selection for stiffness with a restriction of no change in FL (scenario E) would have a similar outcome to selection based on stiffness alone. Selection based on both diameter and stiffness with a restriction of no change in FL (scenario F) would have similar results to scenario C, the corresponding scenario without the restriction, except for extremely little change in RFW.

Scenario C resulted in the highest profitability, and selection based on stiffness alone the lowest profitability. Use of an index combining diameter and stiffness, but with a restriction of no change in FWT (scenario G) would have similar results to scenarios C and F. Comparison of the seven scenarios indicated that selection based on diameter alone, stiffness alone or both would have limited impact on fibre traits, but selection based on diameter alone would have a substantial adverse effect on stiffness, and vice versa. In addition, selection based on a combined diameter and stiffness index with restriction on FL or FWT seems to have similar profitability.

Table 3 Expected responses of diameter, modulus of elasticity (MOE), cross-sectional average RFW, TFW, FWT, FC, FL, and profitability (economic gain) under 1% selection intensity (i=2.67) with selection based on: A) diameter alone; B) MOE alone; C) economically weighted diameter and MOE; D) diameter alone with a restriction of no change in FL; E) MOE with a restriction of no change in FL; F) economically weighted diameter and stiffness with a restriction of no change in FL; G) economically weighted diameter and MOE, with a restriction of no change in FWT.

	Expected response							
Scenario	Diameter (mm)	MOE (GPa)	RFW (μm)	TFW (μm)	FWT (μm)	FC (μg/m)	FL (mm)	Profitability
A	20.68 (19.1%)	-1.18 (-9.6%)	0.96 (3.3%)	0.50 (1.8%)	-0.06 (-2.9%)	-1.02 (-0.3%)	-0.02 (-1.1%)	8.88
B	-14.99 (-13.8%)	1.80 (14.7%)	-1.07 (-3.6%)	-0.43 (-1.6%)	-0.14 (6.6%)	10.88 (3.3%)	0.03 (1.4%)	3.01
C	11.42 (10.5%)	0.02 (0.2%)	0.44 (1.5%)	0.29 (1.1%)	0.05 (2.2%)	10.18 (3.1%)	-0.002 (-0.1%)	11.59
D	20.54 (18.9%)	-1.22 (-10.0%)	1.01 (3.4 %)	0.53 (1.9%)	-0.07 (-3.2 %)	-0.15 (0%)	0.0 (0%)	8.34
E	-15.21 (-14.0%)	1.83 (14.9%)	-1.46 (-5.0%)	-0.47 (-1.7%)	0.16 (7.3%)	9.30 (2.8%)	0 (0%)	3.09
F	11.22 (10.3%)	0.04 (0.3%)	-0.01 (-0.0%)	0.29 (1.0 %)	0.05 (2.1%)	8.40 (2.5%)	0 (0%)	11.57
G	11.21 (10.3%)	0.04 (0.3%)	0.32 (1.1%)	0.25 (0.9%)	0 (0%)	9.80 (3.0%)	-0.00 (-0.0%)	11.57

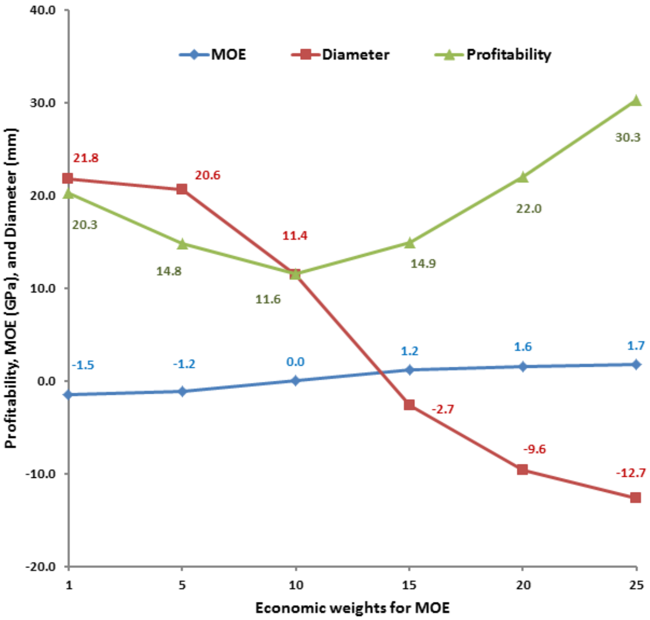


Figure 11 Expected responses of diameter, modulus of elasticity (MOE), and profitability to selection based on diameter (DBH) and stiffness (MOE) with indicated economic weights for MOE relative to DBH under a selection intensity of 1% (i=2.67). The x-axis indicates economic weights for MOE relative to a constant economic weight (1) for diameter.

Breeding to improve wood stiffness (MOE) as well as growth in commercial Swedish Norway spruce populations is highly important due to the strong negative genetic correlation between DBH and MOE. To examine the importance of the relative weights of DBH and MOE, we applied economic weights for MOE varying from 1 to 25 relative to diameter in further analyses (Figure 11). As the economic weighting of MOE declined from the default 10 to 1, the gain for MOE fell by about 1.5 GPa while the gain for DBH increased to 21.8 mm, and profitability increased from 11.6 to 20.3. When the weighting for MOE increased to 20 (a 100% increase in the weighting for MOE relative to DBH, based on mean annual increment per cubic metre per hectare), the gain for MOE increased by about 1.6 GPa and profitability increased to 22.0 while the DBH decreased by 9.6 mm. As the economic weight for MOE increased to 25 relative to DBH, the profitability increased to 30.3 while the genetic gain of DBH decreased by 12.7 mm and MOE increased by 1.7 GPa.

5 Conclusions and Future Perspectives

Based on the six papers in this thesis, following conclusions can be drawn with future perspectives:

1. Wood density declines initially from the pith then increases with age, in contrast to the pattern in pine, in which density typically rises continuously from the pith with no initial decline.

2. Heritability of MFA is low and declines with age after an initial rise, while heritabilities of wood density and MOE initially rise continuously and then remain stable.

3. Combinations of acoustic velocity and Pilodyn penetration measurements on standing trees can be used to efficiently predict MOE.

4. An implemented EM algorithm that includes adjustments for distributions of intact and broken fibres provides more accurate estimates of FL in increment cores than other tested options.

5. Spatial analysis can improve heritability estimates for growth traits (i.e. diameter and height) and the accuracy of breeding value predictions, and thus should be widely applied in analyses of progeny trials.

6. Strong type B genetic correlations in solid wood quality and fibre dimension traits indicate that G × E interaction in these traits may not be important in the Norway spruce breeding program in southern Sweden.

7. There was more G × E interaction in growth traits than in wood quality traits. Frost damage could explain most of the substantial G × E interaction in tree height of Norway spruce in southern and central Sweden.

8. Early selection in the breeding program would be highly effective from ring 10 for diameter, from ring 6-7 for solid wood quality traits (wood density, MFA, and MOE), and from ring 5-10 for fibre dimension traits.

9. There are strong adverse genetic correlations between diameter and solid wood quality traits, so selection based on diameter alone will considerably impair solid wood quality traits.

10. Adverse genetic correlations between diameter and fibre dimension traits are weak to moderate. Selection based on stem diameter growth alone will have a negligible or minor negative effect on FL and a moderate effect on fibre wall thickness.

11. A selection index based on both diameter and stiffness (which should have minimal impact on FL) is recommended for spruce breeding, but appropriate economic weights for growth and stiffness traits should be determined for use in the Norway spruce breeding program.

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Acknowledgements

First, I would greatly thank my main supervisor, Professor **Harry X. Wu**, giving me such nice chance to do quantitative genetics in one of the world leading centres for plant breeding, UPSC in Umeå, Sweden. I am very proud of to be the first PhD student for professor Wu in Sweden. He taught me how to focus on the research in forest breeding and how to deal with statistics and recognize my life. Anyway, he is one of the nicest people who I have met previously.

Rosario Garcia Gil is one of my co-supervisors, she taught me how to write manuscript and how to communicate with other people.

Karlsson Bo, as one of my co-supervisors, you help me a lot how to understand those Skogfork data and explain breeding strategy in Sweden. Meanwhile, thanks for your contribution for my PhD study.

Björn Sundberg is one of my co-supervisors. I would greatly thank you for your contribution in early design of my PhD project.

I would greatly thank **Ewa Mellerowicz** for your contribution for two of my thesis papers. I learnt a lot from you about how to do research.

Ander Fries, you are my best friend, not one of the best in Sweden. Even you are not my co-supervisor, but except Harry, you supervised me mostly from every field. We are even a nice team for bird race in Umea. You taught me go to skiing for cross-country and driving.

David Hall and **Henrik Hallingbäck,** you are my specific colleagues. You started you Postdoc before I came to Harry’s group. I always learn from you including languages-Swedish and English. Thank you very much.

Thank your **Zhou Hong, Qifu Luan, Ruiqi Pian** for your help including the field works and discussion about our future.

Ilka Abreu and Haleh Hayatgheibi, you are my best officemates. We keep our office more quiet than other room.

I would thank **Sonali Sachin Ranade, Ainhoa Calleja-Rodriguez, Irena Fundova, Tomas Funda, Hong Nguyen, Jenny Lundströmer and Maximiliano Kawahata Pagliarini** for your helps from many aspects.

In our department, I should greatly thank our administrators (**Inga-Lis Johansson and Gun-Britt Langnabba).** You are too nice for everyone. Whenever I need help, you always be there and help me!

I thank all my co-authors and colleagues in our Department of Forest Genetics and Plant Physiology for your helps, in Skogfork, such as **Johan Westin, Andreas Helmersson, and Bengt Andersson, in Inventia, such as Sven-Olof Lundqvist, Lars Olsson, and Tomas Grahn, and in Umea University, such as Konrad Abramowicz, and Sara Sjöstedt de Luna.**

Finally, I should thank my parents, sister, and brothers support me to do my research in Sweden. Specially, I should thank my two old sisters who spent most of time to take care of parents and let me have a nice time to do research in one of the north most countries in the world.