Quantitative genetics of lodgepole pine (*Pinus contorta*) wood quality traits in Sweden

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Cover: lodgepole pine (*Pinus contorta*) plantation in northern Sweden
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Abstract

Stem bending, breakage, and general instability of lodgepole pine has been a major problem in northern Sweden due to low stem stiffness. The overall aim of this thesis was to evaluate the potential incorporation of wood quality traits into lodgepole pine advanced breeding programs. To achieve this, 823 increment cores were sampled from 207 half-sib families at two progeny trials of lodgepole pine and genetic variations in wood density, microfibril angle (MFA), modulus of elasticity (clearwood stiffness; MOE_s), radial fibre width (RFW), tangential fibre width (TFW), fibre wall thickness (FWT), and fibre coarseness (FC) were characterised.

To quantify genotype by environment interactions (G × E) for growth and stiffness and to evaluate performance of provenances, diameter at breast height (DBH) and dynamic stiffness of standing trees (MOE_{tof}) were studied, using six 33-36 year-old lodgepole progeny trials within three different breeding zones in northern Sweden. To evaluate genetic gains in selection for an early MFA transition from juvenile to mature wood, six different regression functions were fitted to the MFA profile of each tree to delineate the age variation in MFA transition.

Narrow-sense heritability estimates (h^2) ranged from 0.10 to 0.32 for DBH and from 0.18 to 0.76 for wood quality traits. Unfavourable genetic correlations between growth and stiffness were observed, implying that selection for a 1% increase in DBH alone, would confer 5.5% and 2.3% decreases in lodgepole pine MOE_s and MOE_{tof}, respectively.

Results of the studies in this thesis indicate that simultaneous improvement of DBH and stiffness is achievable when an optimal selection index combining both traits is implemented. Additionally, it is possible to select for an earlier MFA transition from juvenile to mature wood, and thus, decreasing the proportion of the log containing juvenile wood in lodgepole pine selective breeding programs. Finally, G × E was only significant for stiffness within the northern most breeding zone. To achieve the highest stiffness for lodgepole pine, provenances of Yukon origin should be planted at lower latitudes and those of British Columbia (BC) origin should be planted at lower elevations within the tested breeding zones.

Keywords: wood quality traits, genetic parameters, index selection, early selection efficiency, lodgepole pine, G × E interaction, microfibril angle (MFA), transition wood, SilviScan

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Dedication

To my mom, Homa, and the Swedish Forestry Industry

The best preparation for tomorrow is doing your best today.
H. Jackson Brown Jr.

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 **Haleh Hayatgheibi**, Anders Fries, Johan Kroon, and Harry X. Wu* (2017). Genetic analysis of lodgepole pine (*Pinus contorta*) solid-wood quality traits. *Canadian Journal of Forest Research*, 47, pp. 1303-1313

II **Haleh Hayatgheibi**, Anders Fries, Johan Kroon, and Harry X. Wu*. Genetic analysis of fibre-dimension traits and combined selection for simultaneous improvement of growth and stiffness in lodgepole pine (*Pinus contorta*) (submitted to *Annals of Forest Science*)

III **Haleh Hayatgheibi**, Nils Forsberg, Sven-Olof Lundqvist, Tommy Mörling, Ewa J. Mellerowicz, Bo Karlsson, Harry X. Wu, M Rosario García-Gil1*. Genetic control of transition from juvenile to mature wood with respect to microfibril angle (MFA) in Norway spruce (*Picea abies*) and lodgepole pine (*Pinus contorta*) (submitted to *Canadian Journal of Forest Research*)

IV **Haleh Hayatgheibi**, Anders Fries, Johan Kroon, and Harry X. Wu*. Estimation of genetic parameters, provenance performances, and genotype by environment interactions for growth and stiffness in lodgepole pine (*Pinus contorta*) (submitted to *Scandinavian Journal of Forest Research*)

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The contribution of Haleh Hayatgheibi to the papers included in this thesis was as follows:

I. Involved in the experimental design and the field sampling, preparation of all increment cores for SilviScan analysis, data analysis and interpretation, writing the manuscript.

II. Involved in the conceiving, designing and the field sampling, preparation of all increment cores for SilviScan analysis, data analysis and interpretation, writing the manuscript.

III. Involved in the experimental design of lodgepole pine study, preparation of lodgepole pine increment cores, performing genetic analysis, interpretation of the results, writing the manuscript

IV. Involved in conceiving, design and field sampling of the study, data analysis and interpretation, writing the manuscript.

1 Introduction

1.1 Lodgepole pine in its native range

Lodgepole pine (*Pinus contorta* Douglas ex Louden) is native to North America, where it grows between latitudes 31° N in Baja California and 64° N in Yukon in Canada, and from sea level to 3900 m of elevation (Koch, 1996; Wheeler & Critchfield, 1985; Critchfield & Little, 1966) (Figure 1).

Lodgepole pine includes three main sub-species (coastal form var. *contorta*, southern inland form var. *murrayana*, and northern inland form var. *latifolia*) (Elfving *et al.*, 2001; Critchfield, 1957)). It covers more than five million hectares of forest land in the United States and 20 million hectares in Canada (Engelmark *et al.*, 2001; Wellner, 1975; McDougal, 1973).

In its natural habitat, lodgepole pine is the major commercial species and its wood and fibre properties are suited for production of high-quality lumber and pulpwood products (Wang & Stewart, 2012; Wu & Ying, 2004). Additionally, it is the most well-known species for its adaptation to frequent forest fires through development of closed, or serotinous cones (Elfving *et al.*, 2001; Engelmark *et al.*, 2001). The cones remain sealed in the environment until they are exposed to high temperatures required for their opening. This enables dense lodgepole pine stands to grow rapidly in the aftermath of a fire (Backlund, 2013; Despain, 2001; Elfving *et al.*, 2001). Local adaptation of lodgepole pine has been widely studied including norm of reaction of provenances (Wu & Ying, 2004), potential climate adaptation (Wang *et al.*, 2006; Rehfeldt *et al.*, 1999), and seed planning zones (Ying & Yanchuk, 2006).

Due to its pioneer characteristics along with a wide range of adaptation (Pfister & Daubenmire, 1973), lodgepole pine has been planted as an exotic species in many countries such as New Zealand (Ledgard, 2001) and Fennoscandia (Elfving *et al.*, 2001).

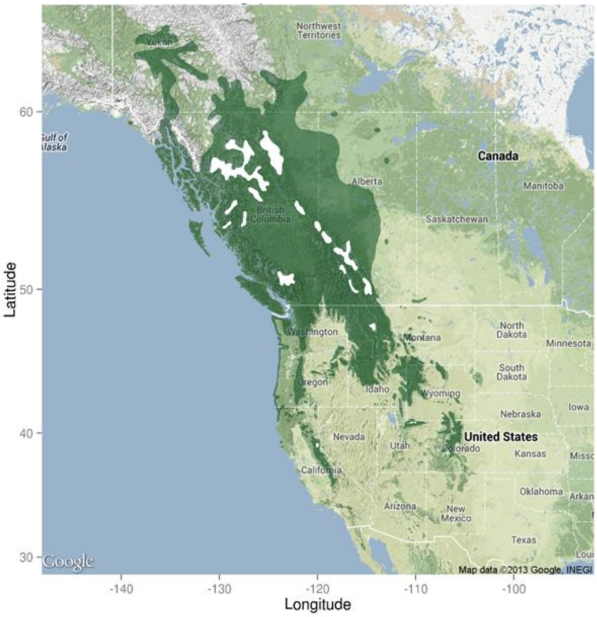

Figure 1. Map of lodgepole pine (*Pinus contorta*) native distribution area (Taysor, 2013)

1.2 Introduction of lodgepole pine into Sweden

Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) are the two most important native tree species for commercial wood production in Sweden. However, during the mid-1960s, a forecast was made that the over-exploitation of old-growth natural forests and the gap in the age-class distribution of Swedish forest stands will lead to a shortage of harvestable timber in the beginning of the next century. This has justified the introduction of exotic tree species as one option to eliminate the anticipated deficit. Later, the choice of lodgepole pine (*P. contorta* var. *latifolia* Engelm.) was supported by the rapid growth and high yield, coupled with desirable wood characteristics and a good survival had been obtained by lodgepole pine in Swedish experimental plantations, between 1910 and 1930 (Elfving *et al.*, 2001; Nellbeck, 1981; Hagner, 1971).

Large-scale introduction of lodgepole pine, primarily as a source of pulpwood, was initiated by extensive series of seed collection and broad research to find the most suitable provenances for Swedish climatic conditions. Therefore, several provenance trials were established from 1962 to 1979 in order to build the basis for seed transfer schemes (Hagner, 1993; Hagner, 1971). Early observations revealed that provenances obtained from interior of British Columbia (BC) and Yukon performed best (Rosvall *et al.*, 1998; Lindgren *et al.*, 1993). It was also discovered that in contrast to the native Scots pine, lodgepole pine populations perform better with a 2-5° northward transfer compared to its latitudinal origin in Canada (Hagner & Fahlroth, 1974).

Furthermore, its superiority in terms of growth, yield, and survival to Scots pine was revealed in the first field studies (Elfving *et al.*, 2001; Elfving & Norgren, 1993; Martinsson, 1983; Hägglund *et al.*, 1979). It has been evidenced that lodgepole pine produces about 36% more stem volume than Scots pine grown under similar conditions in northern Sweden (Elfving *et al.*, 2001). This is driven by several factors, including an earlier start of growth in spring and a lower required heat sum for the initiation of shoot elongation. Additionally, rotation length for lodgepole pine is 10 to 15 years shorter than that for Scots pine (Backlund, 2013; Elfving *et al.*, 2001).

1.3 Lodgepole pine breeding in Sweden

Base material for breeding was collected during the 1970s from the interior of the var. *latifolia* distribution area, located in western Canada, where lodgepole pine was considered to be well-adapted to Swedish conditions. The first plus-tree selections were made from 1970 to 1974 by two forest companies, whereby seed and scions were collected from about 200 plus-trees in natural stands of western Canada. The first clonal and seedling seed orchards covering about 31 hectares were established using these plus trees (Rosvall, 1980). Genetics of these plus-trees have been broadly studied (Fries, 1987).

Later, in order to secure domestic seed sources of lodgepole pine for future demands and long-term breeding purposes, an additional cooperative seed-collection program was launched. Thus, six preliminary breeding zones (utilization zones) in northern Sweden were proposed based on latitude and elevation, mirroring similar climate regions and seed transfer zones (collection zone) in western Canada. About 1112 plus-trees were selected from 100 natural stands (about 12 mother trees from the same stand) distributed in the interior of Yukon, BC, and at some extent in Alberta, and open-pollinated seeds were collected from these selections. Once the collection of seed samples was accomplished, 18 progeny trials (three trials per each breeding zone) from 1979 to 1981, and six seedling seed orchards (per each breeding zone) covering about 100 hectares were established from 1979 to 1987. Based on performance evaluation of these progeny trials at age 10-12 years (Ericsson, 1994), an early genetic thinning for five of these seedling seed orchards was carried out in 1992 (Ericsson & Danell, 1995).

1.3.1 Long term breeding program

Currently, there are a total of 3232 plus-trees available to serve as a founder population for long-term lodgepole pine breeding and conservation. Depending on their origin, these plus trees are divided into three groups (Rosvall *et al.*, 2011) as follows:

1. Old Canadian tested plus-trees (128 trees) which were firstly selected in Canada and then grafted in Sweden
2. Young Swedish untested plus-trees (193 trees) selected in commercial Swedish plantations
3. Young Swedish F1 plus-trees (2911 trees) selected from the best open pollinated families in Swedish progeny tests, which were implemented using plus-trees selected in Canada

The general breeding strategy for lodgepole pine is similar to those of Norway spruce and Scots pine. However, for lodgepole pine, the advanced-generation breeding materials will be divided into 11 populations, each made up of 50 unrelated founder trees, distributed over target areas delineated based on photoperiod (latitude) and temperature gradients (growing season) (Figure 2). The selected breeding parents will be crossed by double pair-mating to form new recruitment populations (Rosvall *et al.*, 2011; Danell *et al.*, 1993).

To date, the breeding program for lodgepole pine in Sweden has mainly focused on improving growth, vitality, and adaptive traits. Several studies estimated genetic parameters for growth, survival, and form traits in Swedish lodgepole pine progeny trials (Ericsson & Danell, 1995; Ericsson, 1994; Fries & Lindgren, 1986). However, wood quality, stem breakage, and general instability of lodgepole pine is a major problem in northern Sweden and needs to be improved. Wood quality traits play a significant role in the health of plantations and are key determinants of economic value of end-use products. Therefore, to enhance the economic value of Swedish lodgepole pine breeding and deployment populations, wood quality traits should be incorporated into the advanced breeding programs. To do so, a rapid, non-destructive, and cost-effective method to measure a large number of sample trees as well as knowledge of quantitative genetic parameters in the large breeding populations are required.

For lodgepole pine, which is an introduced species, it is of vital importance that seed sources are well adapted to their new environmental condition. It is well recognized that the phenotypic response of genotypes might vary when grown under different climatic and edaphic conditions due to genotype by environment interaction (G × E) (Bridgwater & Stonecypher, 1978). Existence of G × E, due to the change in the ranking of genotypes, complicates the design of breeding and deployment strategies. Because tree breeders must decide whether to select for stability of performance, whereby the rate of population improvement is slow, or to select genotypes for specific environments to maximize genetic gain in that site, but with greater program costs (Namkoong *et al.*, 2012). Thus, to implement an effective breeding strategy for lodgepole pine, in the studies this thesis is based upon, genetic parameters of growth, wood quality traits, genetic correlations between traits, and levels of G×E were evaluated.

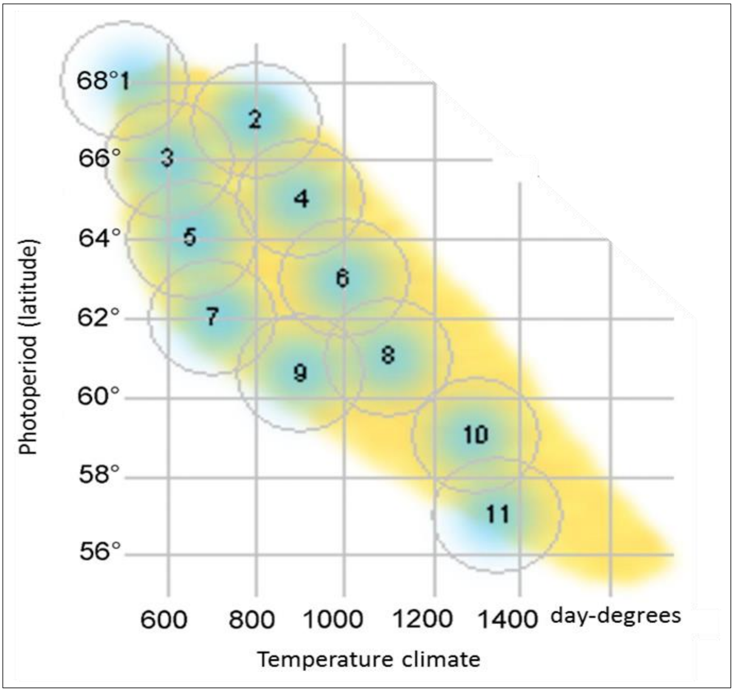

Figure 2. Planned breeding zones for lodgepole pine in Sweden (Rosvall et al., 2011)

1.4 Genetics of wood quality traits

Wood quality traits have become an important focus in advanced tree breeding programs due to their impact on quality of end-use products (Zobel & Jett, 1995; Zobel & Van Buijtenen, 1989). Wood properties exhibit continuous variation, and therefore, are considered as quantitative traits influenced by multiple genetic and environmental factors (Thamarus *et al.*, 2004; Zobel & Jett, 1995). Considerable genetic variation and high heritabilities were reported for most important wood quality traits, including solid-wood and pulp and paper-related traits, in various conifers (Zobel & Jett, 1995). It has also been observed that age by age genetic correlations are very high for wood quality traits, implying early selection for wood quality traits is highly efficient if heritability estimates at early ages are comparable or higher than later ages (Hong *et al.*, 2015; Chen *et al.*, 2014; Lenz *et al.*, 2011; Wu *et al.*, 2007).

1.4.1 Solid-wood traits

Wood density and microfibril angle (MFA) are key indicators of wood quality due to their impact on wood strength, dimensional stability of structural lumber, and pulp quality. Wood stiffness (generally expressed as modulus of elasticity: MOE) and longitudinal shrinkage, are largely dependent on MFA (Cave & Walker, 1994; Zobel & Van Buijtenen, 1989; Cave, 1968). MFA is the angle at which the cellulose microfibrils in the secondary cell wall deviate from the long axis of the cell (Donaldson, 2008; Walker & Butterfield, 1996) (Figure 3).

Several studies in conifers have shown that very large angles of MFA (about 45°) are common in the first 5 to 10 growth rings near the pith (Donaldson, 2008) and MFA values decline gradually until they stabilize at values of 10-15° towards the bark (Moore *et al.*, 2014). Higher MFA and lower stiffness in rings near the pith have been hypothesized to ensure flexibility of young stems to bend through large angles and protect them from wind damage and snow loading (Lichtenegger *et al.*, 1999; Booker & Sell, 1998).

Genetics of wood quality traits have been extensively studied in recent years (Wu *et al.*, 2008). Narrow-sense heritability estimates are generally greater for wood quality traits than for growth traits, whereby heritability estimates of wood density is reportedly greater than those of MFA and MOE (Chen *et al.*, 2014; Hong *et al.*, 2014; Lenz *et al.*, 2010; Baltunis *et al.*, 2007). Estimated genetic correlations of wood density and stiffness with growth traits were highly unfavorable in radiata pine (*P. radiata* Don) (Wu *et al.*, 2008; Baltunis *et al.*, 2007), Norway spruce (Chen *et al.*, 2014), Scots pine (Hong *et al.*, 2014), and white spruce [*P. glauca* (Moench) Voss] (Lenz *et al.*, 2011).

Due to such unfavorable genetic correlation, simultaneous improvement of growth and wood quality traits remains as a constraint in tree breeding programs (Wu & Sanchez, 2011). As such, several methods including designing effective breeding strategies (Hallingbäck *et al.*, 2014; Yanchuk & Sanchez, 2011), using restricted index selection (Chen *et al.*, 2016; Gapare *et al.*, 2009), and applying index selection with optimal economic weights (Ivković *et al.*, 2010; Ivković *et al.*, 2006), have been proposed.

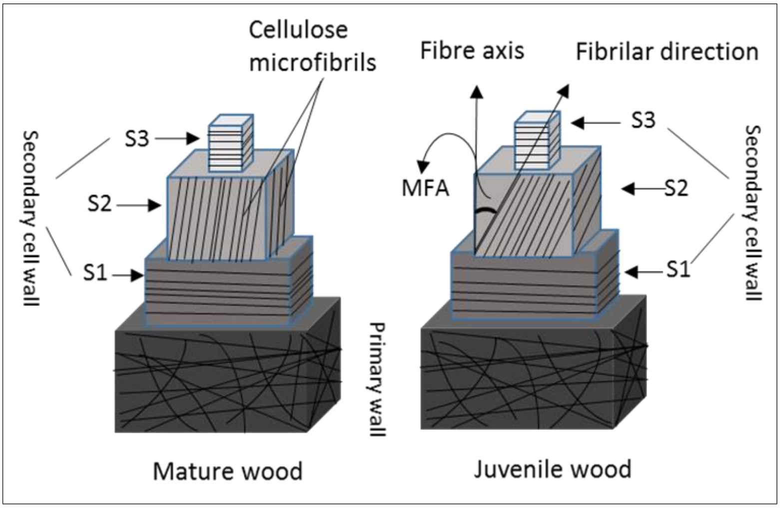

Figure 3. Schematics of microfibril angle (MFA) in juvenile wood and mature wood

1.4.2 Pulp and paper-related traits

Along with wood density, different characteristics of wood fibres, such as fibre length, fibre coarseness (FC), and fibre wall thickness (FWT) are key determinants of pulp and paper quality (Kibblewhite, 1999; Paavilainen, 1993). FC, a commonly used assessment in pulping, defined as fiber mass per fiber length, is strongly related to wall thickness, fiber width and cell wall density (Carrillo *et al.*, 2015; Mansfield & Weineisen, 2007*b*). Thin-walled fibres with low coarseness (e.g., in juvenile and earlywood) result in superior sheet formation and surface properties, while coarse fibers (e.g., in latewood) produce strong paper products (Lenz *et al.*, 2011). Considerable genetic variations and strong inheritances have been reported for tracheid characteristics in conifers (Ivković *et al.*, 2006; Zobel & Jett, 1995).

It has also been noted that density has a negative and unfavorable genetic correlation with radial fiber width (RFW) (Chen *et al.*, 2016; Lenz *et al.*, 2010; Ivković *et al.*, 2006; Hannrup *et al.*, 2000), while it has a strong positive correlation with FWT and FC (Chen *et al.*, 2016; Hong *et al.*, 2014; Lenz *et al.*, 2010). This implies that breeding for density, which enhances the pulp yield, may produce tracheids with smaller diameters and thicker walls, and thus, will lead in inferior paper-sheet formation and surface properties (Lenz *et al.*, 2010).

1.4.3 Juvenile and mature wood characteristics

Differences between juvenile and mature wood are the major sources of variation in wood quality, both among and within trees (Zobel & Sprague, 1998). Such differences occur in various wood characteristics, including specific gravity, mechanical properties (Bendtsen & Senft, 1984), cell length (Yang *et al.*, 1986; Shiokura, 1982), and pulp yields (Zobel & Sprague, 1998). Juvenile wood is mostly undesirable due to its short cells, low density, low strength, high content of compression wood, large MFA, low crystallinity, and high variability compared to mature wood (Barnett & Jeronimidis, 2009; Mellerowicz *et al.*, 2001; Zobel & Van Buijtenen, 1989).

The proportion of juvenile wood in trees is influenced by both genetic and environmental factors and thus is amenable to selection and breeding (Zobel & Sprague, 1998). In addition to selecting genotypes with improved juvenile wood properties, it is also possible to breed for an earlier transition from juvenile to mature wood (Koubaa *et al.*, 2007; Gapare *et al.*, 2006; Loo *et al.*, 1985). Transition from juvenile to mature wood usually occurs over two to five growth rings, depending on the wood property (Alteyrac *et al.*, 2006). However, it is difficult to estimate this boundary with adequate reliability as there is usually no clear demarcation line between juvenile wood and mature wood in a tree stem (Mutz *et al.,* 2004; Zobel & Sprague, 1998).

The distinction between juvenile wood and mature wood has mostly been determined by analyzing trends of radial variation (from pith to bark) for different wood properties such as density (Mansfield *et al.*, 2007*a*; Alteyrac *et al.*, 2006), MOE (Wang & Stewart, 2013), fibre length, and MFA (Wang & Stewart, 2012; Mansfield *et al.*, 2009; Bhat *et al.*, 2001). This method is called threshold or graphic method whereby plots of each wood property are visually evaluated to locate a ring number or age when the property reaches the threshold value for mature wood (Clark *et al.*, 2006). An alternative approach is to use mathematical methods such as segmented regression (Abdel-Gadir & Krahmer, 1993; Szymanski & Tauer, 1991) or segmented non-linear models (Alteyrac *et al.*, 2006; Mutz *et al.*, 2004).

In study III, MFA was used to evaluate genetic control of transition from juvenile to mature wood in lodgepole pine and Norway spruce.

2 Objectives

The overall objectives of the studies this thesis is based upon, were to estimate genetic parameters for growth and wood quality traits of lodgepole pine in Sweden and to evaluate selective breeding strategies that incorporate solid-wood and fibre related traits into lodgepole pine advanced breeding programs. The following specific questions were addressed:

1) How large is the genetic variation for solid-wood (I), and pulp and paper related traits (II) and what are their genetic relationships with growth traits (papers I and II)?
2) How can solid-wood and fibre traits be incorporated into selective breeding programs, and how much gain will be obtained for these traits using different selection indices incorporating wood quality traits (paper I and II)?
3) Is there any genetic gain in selection for earlier transition from juvenile to mature wood with respect to MFA (paper IIII)?
4) How large is G × E for growth and stiffness and how is the performance of provenances in different breeding zones of lodgepole pine (paper IV)?

3 Materials and Methods

3.1 Field trials

Six lodgepole pine open-pollinated progeny trials within breeding zone two (Jovan and Mader), planted in 1981; breeding zone four (Hemmingen and Övra), planted in 1980; and breeding zone five (Lagfors and Hemmesmark), planted in 1979 were selected for the studies underlying this thesis (Figure 4. A).

Trials Mader and Jovan originated from four provenances in Yukon (Carmacks, Frances Lake, Watson Lake, and Whitehorse), trials Övra and Hemmingen originated from three provenances in BC (Fort St. John, Prince George, Fort Nelson) and one provenance in Yukon (Watson Lake), and trials Lagfors and Hemmesmark originated from two provenances in BC (Fort St. John and Prince George) (Figure 4. B).

The experimental design for each trial was a randomized complete block layout with five replicates. Each family was planted in 10 (column) x 12 (row) tree plots within each block. Tree spacing was 2 m between rows and 1.5 m within rows. Trials within each breeding zone included ~ 200 common half-sib families, while there were no common families among breeding zones.

In addition, two 21-year-old Norway spruce progeny trials, S21F9021146 aka F1146 (trial 1) and S21F9021147 aka F1147 (trial 2), comprised of 1,373 and 1,375 half-sib families, respectively, located in southern Sweden, were utilized in study III. Both trials were planted as randomized incomplete blocks with single-tree plots at spacing of 1.4 m × 1.4 m (Chen *et al.*, 2014).

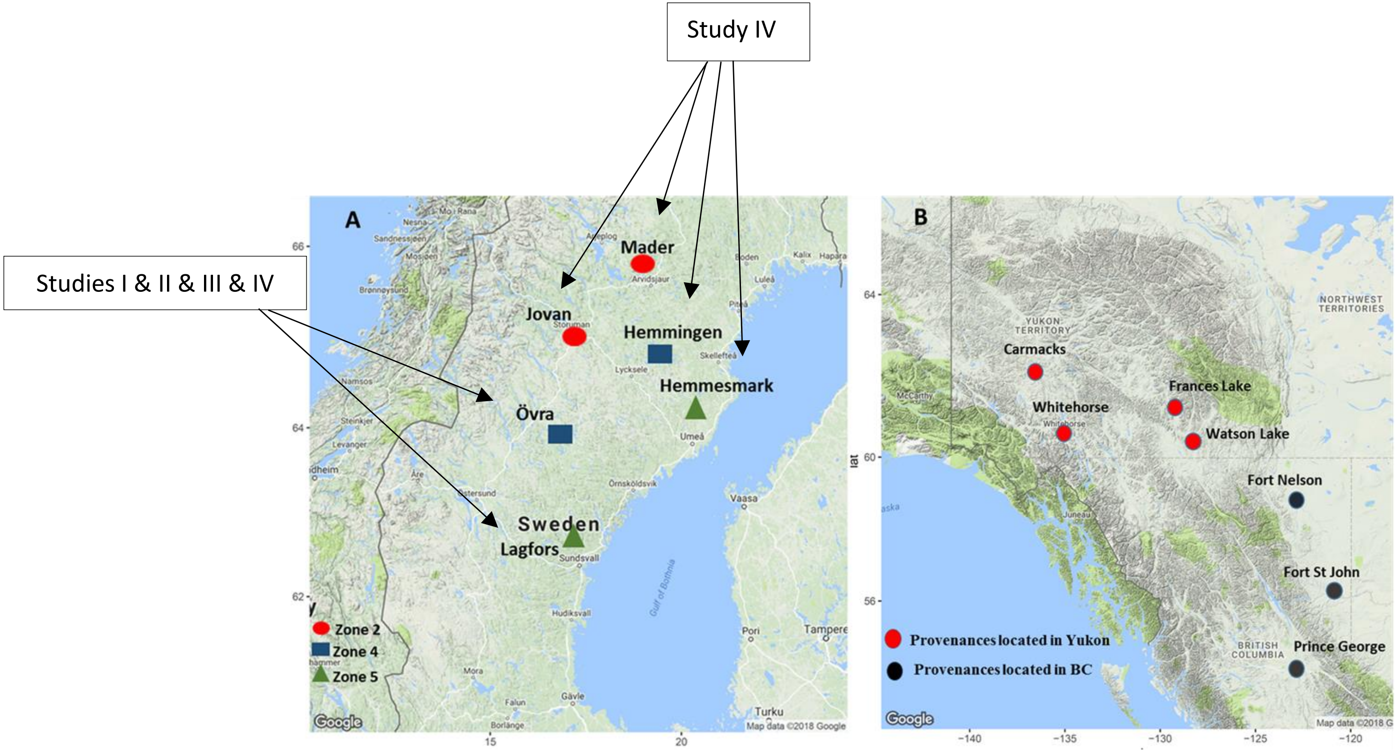

Figure 4. Locations of six lodgepole pine progeny trials (within three breeding zones) in northern Sweden (A) and their seed origins (provenances) distributed in Yukon and British Columbia (BC) in Western Canada (B).

3.2 Studied traits and non-destructive measurements

3.2.1 SilviScan measurements

Bark-to-bark increment cores (12 mm) were collected at 1.3 m height from 399 trees at Övra (approximately four trees from 100 families) and from 424 trees at Lagfors (approximately four trees from 107 families) and assessed using a SilviScan instrument (Innventia, now part of RISE, Stockholm, Sweden). Before the SilviScan measurement, each increment core was sawn into a 7 mm high × 2 mm thick radial strip from pith to bark. High-resolution pith-to-bark radial variations for three solid-wood quality traits (wood density, MFA, and modulus of elasticity (clearwood stiffness; MOE_S)) addressed in paper I, and four fibre traits (RFW, tangential fibre width (TFW), FC, and FWT) addressed in paper II, were obtained (Table 1). Density was obtained as an average for 25 µm radial intervals, while MFA was averaged over 2 mm intervals, and these estimates were used to predict MOE_s (Evans, 2006).
Norway spruce increment cores were collected at breast height from 5,618 trees and high-resolution radial variations in MFA from pith to bark were measured for each core, using SilviScan (study III).

3.2.2 Acoustic velocity measurement

The Hitman ST300 tool (Fibre-gen, Christchurch; New Zealand) (Figure 5) was used to measure acoustic velocity of about 7500 standing trees within 324 half-sib families, addressed in studies I and IV. Two sensor probes were inserted into the outer wood of the tree, with the lowest probe at around 1 m high. Probes were placed in sections of the stem that had fewer branches and were vertically aligned at a distance of about 70 to 110 cm apart. The distance was measured with a laser beam, and an acoustic wave was passed through the stem by striking the transmitter probe with a steel hammer. The wave was picked up by the receiver probe and its time of flight (tof) was recorded. Two series of eight hits were taken per tree, and an average of two measurements was taken. Dynamic MOE (MOE_{tof}) was estimated using the product of squared sound velocity (m/s) multiplied by a constant green density of 1000 (kg/m3) (Wang *et al.*, 2001).

Table 1. *Solid-wood and fibre wood SilviScan measurements and their abbreviations*

SilviScan measurements	Abbreviation	Method of determination
Wood Density	Density	X-ray densitometry
Radial fibre width	RFW	Image analysis
Tangential fibre width	TFW	Image analysis
Fibre coarseness	FC	Calculate with RFW, TFW and Density
Fibre wall thickness	FWT	Calculate with RFW, TFW and Density
Microfibril angle	MFA	X-ray diffraction
Modulus of elasticity	MOE_s	X-ray diffraction and density

Figure 5. Hitman ST300 tool used to measure the acoustic velocity of standing trees

3.3 Statistical analysis

3.3.1 General model

All the statistical analysis were done using ASReml statistical software package (Gilmour *et al.*, 2009). To estimate genetic and phenotypic parameters and correlations, both univariate and multivariate mixed-linear models were used. The general univariate model equation is:

$$y = Xb + Zu + e$$

Where y is the vector of each individual tree observation, b is the vector of fixed effect, u is the vector of random effect and e is the vector of residuals. X and Z are the incidence matrices of fixed effect (b) and random effect (u), respectively. Bivariate models were used to estimate genetic and phenotypic correlations between two different traits (papers I, II, IV), age-age correlations (papers I and II), and type-B genetic correlations (genetic correlations for the same trait in different sites) (paper IV).

3.3.2 Index selection

Variance-covariance matrices for diameter at breast height (DBH) and MOE were estimated using multivariate linear mixed models. The Smith-Hazel selection index (Hazel, 1943; Smith, 1936) with different sets of economic weights for MOE$_s$, ranging from 5 to 15 relative to 1 for DBH, was applied (paper II). The index is written as follows:

$$I = b_1 P_{DBH} + b_2 P_{MOE}$$

Where P_{DBH} and P_{MOE} are an individual tree's measurement of DBH and MOE$_s$, respectively, b_1 and b_2 are their respective index coefficients. The index coefficient (b) was obtained as follows:

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

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.

The expected genetic gain (ΔA) of each individual trait included in a Smith-Hazel index was calculated as:

$$\Delta A_x = i \frac{(b_x V_{Ax} + b_y COV_{Axy})}{\sigma_I}$$

where ΔA_x is the expected genetic gain in trait x, i is the selection intensity of 1% (i=2.67), V_{Ax} is the additive genetic variance of trait x , COV_{Axy} is the additive genetic covariance of trait x and associated trait y, b_x and b_y are the index coefficients generated from the Smith-Hazel index, and σ_I is the phenotypic standard deviation of the index.

3.3.3 Model fit and determination of transition age

In the study described in paper III, the radial patterns for MFA of all 5618 Norway spruce and 823 lodgepole pine individual trees were plotted against the cambial age. However, there were some individuals for which the general decreasing trend of MFA from pith to bark had been changed, due to some disturbances such as compression wood. Therefore, such outliers (abnormal curves) were identified and excluded prior to data analysis, as follows:

1) Exclusion_1 or basic method: exclusion of those individuals for which MFA values increased with cambial age. This was the baseline of data treatment and thus the first step of following exclusions 2 and 3.

2) Exclusion_2 or shape-based method: following the basic method, annual rings of the individuals for which average MFA values were greater than their three previous rings average MFA value, were removed.

3) Exclusion_3 or family-based method: following the baseline method, annual rings of the individuals, which had average MFA values deviating from their corresponding family-mean MFA values by more than 1.96 × SD, were excluded from data analysis.

After removal of outliers, six different regression functions were fitted to the pith-to-bark MFA profiles of the individual trees. A threshold value of 20° was considered for MFA and when the parameter of the fitted functions fell below the threshold, the estimated parameter was defined as MFA transition.

Norrrow-sense heritability estimates and genetic gains in direct selection of MFA transition were obtained for both species.

4 Results and Discussion

4.1 Traits summary

Mean values, coefficients of variation, and narrow-sense heritability estimates (h^2) for DBH and stiffness measured acoustically ($\mathrm{MOE_{tof}}$) at the six sites are presented in Table 2 (Paper IV), and nine wood quality traits obtained based on benchmark SilviScan using two sites are presented in Table 3 (Paper I and II). In general, coefficient of additive (CV_A) and phenotypic (CV_p) variations were higher for DBH than for wood quality traits, except for MFA. Such pattern had been previously reported in various conifers (Chen *et al.*, 2014; Hong *et al.*, 2014; Gaspar *et al.*, 2008). For DBH, CV_A ranged from 7.4% to 13.7% with the highest value obtained at Hemmesmark and the lowest obtained at Lagfors. For $\mathrm{MOE_{tof}}$, CV_A ranged from 7.2% to 11.8% with the highest value obtained at Mader and the lowest obtained at Lagfors (Table 2).

For SilviScan-based solid-wood quality traits, the highest CV_A and CV_p were obtained for MFA and $\mathrm{MOE_s}$ at Övra. Similarly, CV_A and CV_p were the highest for MFA at Lagfors, while CV_A for $\mathrm{MOE_s}$ was significantly lower at Lagfors. Among fibre traits, FC was the most variable trait at both trials while TFW had the lowest CV_A and CV_p (Table 3). In accordance with results of other studies for conifers, such as Norway spruce (Chen *et al.*, 2016) and Scots pine (Hong *et al.*, 2014), solid-wood traits were generally more variable than fibre traits, particularly for MOE.

Table 2. *Number of observations (N), mean values, coefficients of additive (CV_A) and phenotypic (CV_p) variation and narrow-sense heritability (h^2) for growth and acoustic stiffness of six lodgepole pine progeny trials within three breeding zones (parameters presented in paper IV).*

Trial	Trait									
	DBH (mm)					MOE_{tof} (GPa)				
	N	Mean	CV_A (%)	CV_p (%)	h^2	N	Mean	CV_A (%)	CV_p (%)	h^2
Mader	1943	132	11.8	20.8	0.32 (0.09)	1174	11.2	11.8	17.8	0.44 (0.11)
Jovan	5547	116.8	9	21.8	0.17 (0.03)	1241	13.7	8.6	12.4	0.47 (0.11)
Övra	4329	130.5	7.6	24.3	0.10 (0.04)	1250	13.7	7.2	17	0.18 (0.09)
Hemmingen	4662	114.1	10.8	26	0.17 (0.04)	1242	13.6	9.4	13.9	0.46 (0.11)
Lagfors	6289	128.1	7.4	21.6	0.12 (0.04)	1332	15.9	7.2	14	0.29 (0.10)
Hemmesmark	3129	105.2	13.7	28.7	0.23 (0.08)	1325	15.1	9.4	12.4	0.58 (0.11)

DBH, diameter at breast height; MOE_{tof}, modulus of elasticity of time of flight

Standard errors of heritabilities are in the parenthesis

Table 3. *Mean values, coefficients of additive (CV_A) and phenotypic (CV_p) variation and Narrow-sense heritabilities (h^2) for solid-wood and fibre traits of two lodgepole pine progeny trials (parameters presented in paper II).*

Benchmark SilviScan	Trial							
	Övra				Lagfors			
	Mean	CV_A (%)	CV_p (%)	h^2	Mean	CV_A (%)	CV_p (%)	h^2
Solid-wood traits								
Density (kg/m)	456.6	4.2	8.1	0.29 (0.22)	483.2	5.6	7	0.67 (0.21)
EWD (kg/m)	343.2	4	7.2	0.33 (0.22)	357.2	5.2	6.1	0.77 (0.22)
LWD (kg/m)	735.8	4.3	6.9	0.40 (0.23)	774.4	3.7	6.3	0.39 (0.20)
MOE$_s$ (GPa)	10.4	11.5	21	0.30 (0.20)	12	5.6	15.7	0.13 (0.16)
MFA (°)	18.6	15.2	27.9	0.30 (0.20)	16.6	13.5	23.8	0.33 (0.19)
Fibre traits								
RFW (µm)	31.7	4.6	5.9	0.71 (0.21)	30.9	4	4.7	0.73 (0.20)
TFW (µm)	28.8	2.5	3.9	0.44 (0.21)	28.6	3	3.5	0.74 (0.20)
FWT (µm)	2.4	4	7.8	0.29 (0.21)	2.6	6	7.2	0.72 (0.21)
FC (µg/m)	397.7	5.7	8	0.52 (0.21)	405.9	6.2	7.5	0.72 (0.20)

EWD, early wood density; LWD, latewood density; MOE$_{s,}$ modulus of elasticity; MFA, microfibril angle; RFW, radial fibre width; TFW, tangential fibre width; FWT, fibre wall thickness; FC, fibre coarseness

4.2 Inheritance of growth and wood quality traits

Among the SilviScan-based solid-wood traits, the highest heritabilities were obtained for wood densities at Lagfors, ranging from 0.39 to 0.77, with the highest value obtained for early wood density (EWD) (h^2=0.77), while such estimates ranged from 0.29 to 0.40 at Övra. Heritabilities obtained for fibre traits were generally higher at Lagfors ($h^2 \geq 0.72$), whereas they were lower at Övra (ranged from 0.29 to 0.71). Our heritability estimates were generally higher for wood quality traits than for growth traits, in line with results obtained in other conifers (Chen *et al.*, 2014; Hong *et al.*, 2014; Wu *et al.*, 2008). Further, fibre traits were generally more heritable than solid-wood traits in our study and heritabilities of fibre traits were higher than those reported for Scots pine (Hong *et al.*, 2014), Norway spruce (Chen *et al.*, 2016), and white spruce (Lenz *et al.*, 2010), particularly at Lagfors.

4.3 Correlations among growth, solid-wood and fibre traits

In study I, we found several unfavourable genetic correlations (r_A) between growth and solid-wood traits. SilviScan-based MOE was more negatively correlated with DBH (Figure 6) than those measured acoustically (Hayatgheibi *et al.*, 2017). Such finding had been previously reported, whereby SilviScan-derived MOE was more negatively correlated with DBH, volume and height in Scots pine (Hong *et al.*, 2014) and Norway spruce (Chen *et al.*, 2015).

Among all wood density component traits, the most unfavourable genetic correlation was found between DBH and early wood density (EWD) at both trials. Low to moderate negative genetic correlations, associated with high standard errors, were observed between wood density and DBH. Genetic correlation of density with growth traits was highly unfavourable in radiata pine (Wu *et al.*, 2008; Baltunis *et al.*, 2007), Norway and white spruce (Chen *et al.*, 2014; Lenz *et al.*, 2010; Steffenrem *et al.*, 2009; Ivković *et al.*, 2002), and Scots pine (Hong *et al.*, 2014), but non-significant in maritime pine (*P. pinaster* Ait) (Bouffier *et al.*, 2009) and loblolly pine (*P. taeda* L.) (Antony *et al.*, 2013).

It is well known that MOE is correlated with density and MFA (Wu *et al.*, 2007). However, MOE_s was less correlated with density in Lagfors (r_A= 0.29) than in Övra (r_A= 0.65). Further, MFA had a moderate to high negative, but favourable genetic correlation with MOE_s and MOE_{tof} at both trials and very high genetic correlations were observed between MOE_s and MOE_{tof} (r_A ~ 0.90).

Correlation of fibre traits with growth and solid-wood traits was assessed in paper II. Genetic correlation of DBH with RFW and TFW was moderate, ranging from 0.32 to 0.55, while it was nearly zero with FWT, at both trials. Similarly, DBH had a moderate genetic correlation with FC at Övra, while such correlation was non-significant at Lagfors (study II, Table 2).

The non-significant correlation observed between DBH and FWT for lodgepole pine in our study, is in contrast with previously reported correlations in other conifers. As such, DBH was negatively correlated with FWT in Norway spruce (Chen *et al.*, 2016) and Scots pine (Hong *et al.*, 2014), implying that trees with high volume growth tend to have thinner walls and thus lower density. We found a very high correlation between density and FWT at both trials (r_A ~ 0.90), similar to what was reported for Norway spruce (Chen *et al.*, 2016), but higher than those reported in Scots pine and white spruce (Hong *et al.*, 2014; Lenz *et al.*, 2010). In addition, FWT was highly correlated with FC.

Further, density had a moderate negative and unfavourable correlation with RFW and TFW at both trials. Similarly, FWT had a low to moderate negative genetic correlation with RFW and TFW in Övra. This implies that breeding for density, which enhances pulp yield, may produce tracheids with smaller diameters and thicker walls, and thus, will lead in inferior paper-sheet formation and surface properties (Lenz *et al.*, 2010).

In study IV, genetic correlations between DBH and MOE_{tof} for single-site and combined-site analysis were obtained. We found that growth-stiffness genetic correlation is more unfavourable in breeding zone two (Mader and Jovan) and four (Övra and Hemmingen), while such correlations were non-significant in breeding zone five (Lagfors and Hemmesmark). Results were shown in Table 4 and 5 in study IV.

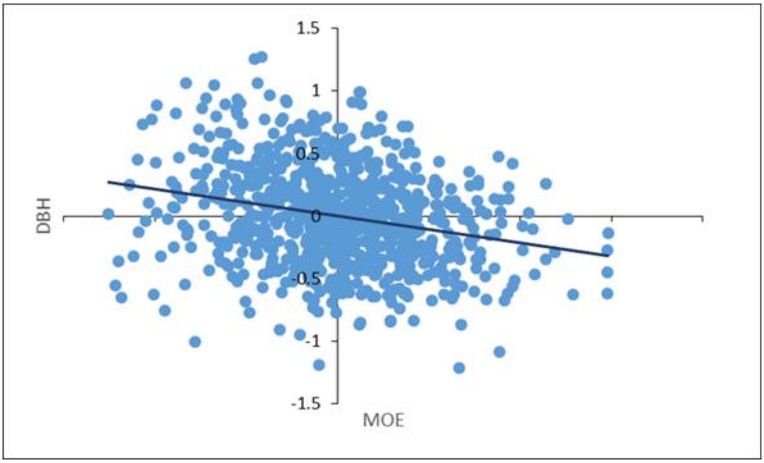

Figure 6. Scatter plot of lodgepole pine individual trees breeding values for diameter at breast height (DBH) and modulus of elasticity (MOE)

4.4 Age-age correlations and efficiency of early age selection for growth and wood quality traits

Age-age genetic correlations from early ages to the reference age of 26 years were very high for solid-wood (paper I) and fibre traits (paper II) in lodgepole pine, reaching 0.9 at cambial age four for MFA and FC; cambial age six for RFW and TFW; and cambial age 10 for MOE and ring width in both trials. Age-age genetic correlations for density and FWT in Övra reached unity at cambial age four, while such correlation obtained at age 10 in Lagfors. Due to the high age-age genetic correlation and high heritability estimates obtained for wood quality traits, we observed that early selection is very effective for wood quality traits in lodgepole pine.

Among all studied traits in this thesis, MFA had the highest early selection efficiency as the heritability estimates and age-age genetic correlations obtained at early ages were very high for this trait. Such a high early selection efficiency for MFA as early as age four had also been previously reported in Norway spruce (Chen *et al.*, 2014) and white spruce (Lenz *et al.*, 2011). Furthermore, we found that early selection for wood density, MOE, and fibre traits is optimal at about cambial ages of eight to 10 years in lodgepole pine, similar to what was found in Scots pine (Hong *et al.*, 2015). It is known that early age selection is more efficient for wood quality traits than for growth traits in conifers owing to the higher heritability estimates at early ages and higher age-age correlation obtained for wood quality traits compared to growth traits (Hong *et al.*, 2015; Chen *et al.*, 2014; Wu *et al.*, 2007; Li & Wu, 2005). Similar pattern was observed in our study as selection efficiency for ring width was only about 0.5 at cambial age 14 in Övra and it was nearly zero in Lagfors due to the very low heritability estimate obtained for ring width at the reference age in Lagfors.

4.5 Selection scenarios incorporating wood quality traits

Several selection scenarios for incorporating wood quality traits were studied. Genetic gains and correlated genetic responses for growth and solid-wood (paper I); and fibre traits (paper II), using selection intensity (i) of 2.67 (i.e., 1%) were assessed. Results are presented in Table 4. Selection based on DBH would result in an increase of 7.9 % in DBH, slight increases in fibre traits, but unfavourable -5.5, -2.3, -1.5% changes in MOE_s, MOE_{tof}, and density, respectively (Table 4).

Selection based on MOE_s, would incur increases of 13, 11.4, and 3.2% in MOE_s, MOE_{tof}, and density, respectively, but unfavourable decrease of -6.5 % in DBH, and negligible changes in fibre traits. Due to the unfavourable growth-stiffness genetic correlation obtained in paper I, index selection with appropriate economical weights for simultaneous improvement of these traits was proposed. Economic weights for growth and stiffness in lodgepole pine have not been estimated using production-system parameter estimates. Recent study by Chen *et al.* (2016) in Norway spruce suggested that an increase of 1 GPa in MOE is 10 times as profitable as an increase of 1 mm in diameter, based on the economic weights of growth and MOE used in radiata pine (Ivković *et al.*, 2006).

Therefore, to examine the importance of relative weights of DBH and MOE in lodgepole pine, a selection index with different sets of economic weights for MOE_s, ranging from 5 to 15, relative to 1 for DBH, was applied in our study (paper II). Results are shown in Figure 7. As the economic weighting of MOE decreased from the weight of 10 to 5, the gain for MOE declined to -0.43 GPa, whereas the gain for DBH increased to about 9.5 mm. When the economic weighting for MOE increased to 15, the gain for MOE increased by about 1.1 GPa, while the gain for DBH decreased by about -3.5 mm. We found that the economic weighting of MOE ranging from 7 to 10 resulted in positive genetic gains for both traits.

In the subsequent analysis reported in paper II, we observed that, selection index combining DBH and MOE using economic weights (10 for MOE relative to 1 for DBH) led to slight increases in TFW (1.5%), FWT (3.6%), FC (4.4%), and wood density (2.3%).

Table 4. *Genetic gains (in bold and italic format) and correlated genetic responses for DBH, solid-wood and fibre traits*

Selection trait	**Response (%)**							
	DBH	MOE_s	MOE_{tof}	Density	RFW	TFW	FWT	FC
DBH	***7.9***	-5.5	-2.3	-1.5	2.1	1	0.16	2.5
MOEs	-6.5	***13***	11.4	3.2	-1.6	0.8	3.2	2.8

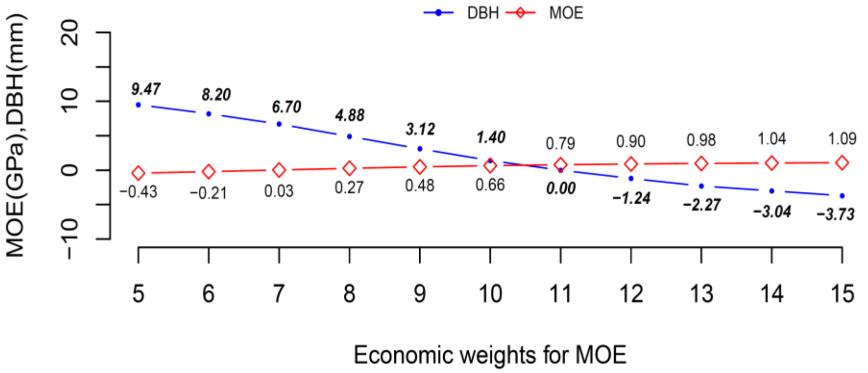

Figure 7. Expected genetic changes of diameter at breast height (DBH) (bold) and modulus of elasticity (MOE) for selection based on DBH and MOE with indicated economic weights for MOE relative to a constant economic weight (1) for DBH (x-axis), under a selection intensity of 1% (i=2.67).

4.6 Genotype by environment interactions and provenance performances

In forestry, G×E has been extensively studied (Li *et al.*, 2017; Matheson & Cotterill, 1990; Shelbourne, 1972) and significant G×E, primarily for growth, has been reported in various important conifers, such as radiata pine (Ivković *et al.*, 2015; Baltunis *et al.*, 2010; Wu & Matheson, 2005), loblolly pine (Roth *et al.*, 2007; Li & McKeand, 1989), slash pine (*P. elliottii* Engelm) (Hodge & White, 1992), and Norway spruce (Chen *et al.*, 2017). According to literature (Apiolaza, 2012; Baltunis *et al.*, 2010; Gapare *et al.*, 2010; Hallingbäck *et al.*, 2008; Wu & Matheson, 2005), G×E for wood quality traits is generally low compared to growth traits.

We observed that type-B genetic correlations (r_b) for growth, stiffness ($\mathrm{MOE_{tof}}$), and survival were mostly high within each breeding zones, except for DBH and survival in the breeding zone four (r_b=0.74 and 0.40, respectively) and for $\mathrm{MOE_{tof}}$ in the breeding zone two (r_b= 0.46), indicating that G × E might not be important in lodgepole pine, except for stiffness in northern Sweden (Study IV). Similarly, results of other studies, investigating the extent of G × E for growth and wood quality traits in Swedish breeding programs revealed that G × E is negligible for wood quality traits in Norway spruce (Chen *et al.*, 2016; Chen *et al.*, 2014; Hallingbäck *et al.*, 2008) and low to moderate for growth in Scots pine (Hannrup *et al.*, 2008).

Previous studies, investigating performance of lodgepole pine provenances in Sweden, had reported that survival is largely dependent on the latitude of origin, whereby seed sources of northern origin had higher survival as well as higher rate of seed production (Lindgren *et al.*, 1994). Additionally, it has been reported that height growth is associated with altitude of origin, whereby fastest growth was achieved for provenances about 800 m, and there was a decline in growth above this threshold (Fries, 1986; Lindgren, 1983)

Relative performance of provenances for DBH and $\mathrm{MOE_{tof}}$ within a test site and within breeding zones were assessed (Study IV). Results were shown in Figures 8 and 9. We found that the mean performance of provenances, particularly for mean DBH, differed significantly within a breeding zone. As such, seed sources originating from Yukon, the northernmost provenances, had better growth performance in higher latitude, particularly provenances Frances Lake and Whitehorse.

In contrast, seed sources originating from BC, had better growth performance when planted at trials with lower latitude within a breeding zone. Furthermore, maximum growth performance of provenances originating from BC, Fort St. John and Prince George in particular, was achieved at Övra, the trial associated with the highest precipitation during vegetative growth and the highest elevation.

In contrast to what was observed for DBH, we found that provenances originating from Yukon, particularly Whitehorse, had the lowest mean stiffness at Mader (higher latitude), and the highest mean stiffness of seed sources originating from BC (Fort St. John and Prince George) was obtained when planted at Lagfors and Hemmesmark, trials which had the warmest temperatures and the lowest elevations.

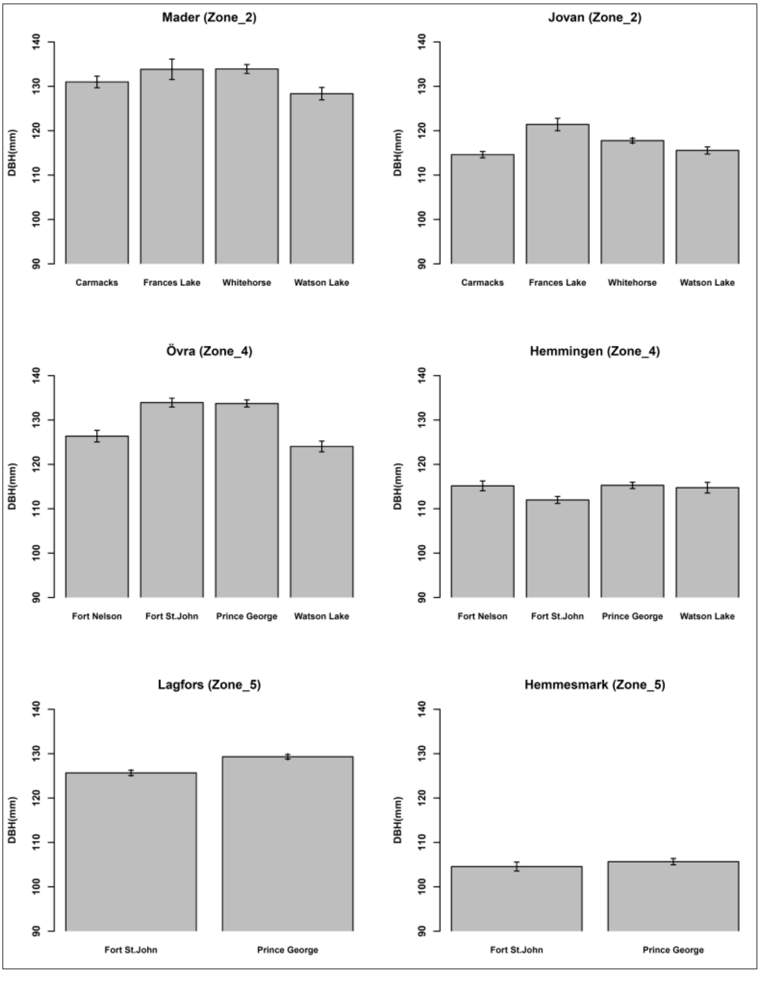

Figure 8. Diameter at breast height (DBH) (mm) means for provenances of lodgepole at the six progeny trials (within three breeding zones) in northern Sweden. The vertical lines in the middle of the boxes are error bars.

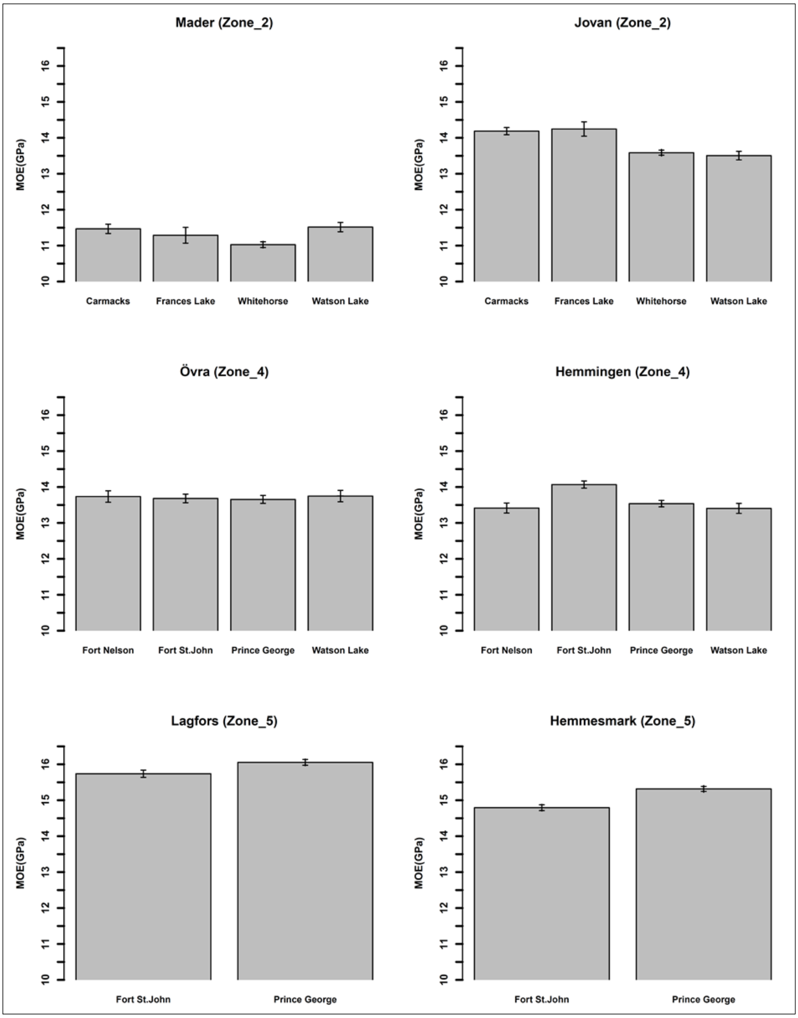

Figure 9. Modulus of elasticity (MOE) (GPa) means for provenances of lodgepole at the six progeny trials (within three breeding zones) in northern Sweden. The vertical lines in the middle of the boxes are error bars.

4.7 MFA transition from juvenile to mature wood

4.7.1 MFA radial variation

For both lodgepole pine and Norway spruce, the MFA average profiles decreased from above 30° close to the pith towards about 10° close to the bark (Figure 10). In Norway spruce, mean MFA profile decreased from about 30° at the pith and then stabilized after reaching a cambial age of 10 years at about 10° in Höreda and about 12° in Erikstorp. The mean MFA profile for lodgepole pine started at 40° followed by a rapid decrease to about 30° after 3 years, after which the shape of the development was similar to that for Norway spruce but slower, stabilizing after cambial age of 15 years at about 12° in Övra and about 10° in Lagfors.

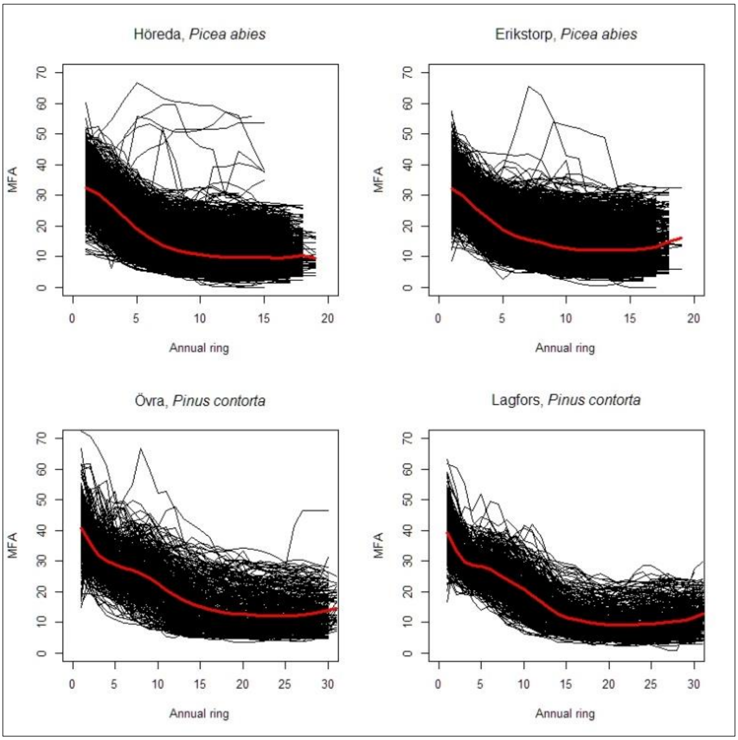

Figure 10. Radial trends for MFA of Norway spruce at two trials (Höreda and Erikstorp) from cambial age 1 to 20 and for *Pinus contorta* at two trials (Övra and Lagfors) from cambial age 1 to 30. The black lines represent the actual observations from all individual trees and the red line is the mean radial variation of MFA against the cambial age.

4.7.2 Heritability estimates and genetic gains

Heritability estimates obtained for lodgepole pine MFA transition were greater than those obtained for Norway spruce (paper III, Table 1). Moreover, in both species, heritabilities were generally highest based on the slope function, while they were lowest based on the logistic function, under all exclusion methods. Heritabilities ranged from 0.08 to 0.23 for Norway spruce, with the highest value obtained based on the slope function under exclusion_2 and the lowest value obtained based on the logistic function under exclusion_3.

For lodgepole pine, all heritability estimates were nearly zero based on the logistic function. This is driven by the inability of this function to estimate MFA transition, using the threshold value of 20°. In general, heritabilities ranged from 0.15 to 0.53 in Övra and from 0.22 to 0.43 in Lagfors (logistic function was excluded). In addition to the slope function, high heritabilities were obtained based on the central peak (ranging from 0.33 to 0.38) and negative exponential functions (ranging from 0.26 to 0.34) in Övra, and based on the arctangent (ranging from 0.41 to 0.43) and polynomial (ranging from 0.36 to 0.38) in Lagfors.

As was observed for heritability estimates, genetic gains obtained based on the slope function were highest, while those obtained based on the logistic function were lowest, regardless of which exclusion method was applied. In addition to the slope function, high genetic gains were obtained based on the negative-exponential and central peak functions in Norway spruce and based on arctangent and negative-exponential functions in lodgepole pine (paper III, Table 2).

These findings indicate that it is possible to select for an earlier MFA transition from juvenile to mature in Norway spruce and lodgepole pine selective breeding programs.

5 Conclusions and Future perspectives

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

1) Wood density, MOE_s, latewood proportion (LWP), and values of fibre properties increased from the pith, while MFA and ring width were high around the pith, then gradually decreased and stabilized towards the bark. In general, observed radial age trends were similar at two lodgepole pine trials, though wood density, MOE_s, LWP, FWT, and FC were higher in Lagfors compared to Övra, while ring width, MFA, and RFW were lower, after the cambial age of 18 years.

2) Heritability estimates of wood density and fibre properties were low near the pith, increased until they peaked between the cambial ages of 8-16 years, then stabilized towards the bark. In general, all estimated heritabilities were significantly higher after the cambial age of 4 years in Lagfors, except for its MOE_s heritability estimates, which were lower after the cambial age of 12 years.

3) Early selection at cambial age of 4 years for MFA and about cambial ages of 8-10 years for wood density, MOE, and fibre properties would be highly efficient in lodgepole pine breeding programs.

4) Due to the unfavourable DBH–stiffness genetic correlation, selection for a 1% increase in DBH, would result in decreases of 5.5% and 2.3% lodgepole pine stiffness (MOE_s and MOE_{tof}, respectively). However, Simultaneous improvement of growth and stiffness is achievable when a selection index with 7 to 10 economical weights for stiffness (MOE_s) relative to 1 for DBH is incorporated.

5) Unfavourable relationship between solid-wood and pulpwood traits suggests that breeding strategies must be implemented to improve wood quality of lodgepole pine for multiple uses.

6) There is a possibility to select for an earlier MFA transition from juvenile to mature wood, and thus, decreasing the proportion of the log containing juvenile wood in lodgepole pine selective breeding programs.

7) Although type-B genetic correlations for growth and stiffness were mostly strong, G × E for stiffness was significant within the most northern breeding zone. Furthermore, the low stiffness of lodgepole pine as well as its unfavourable genetic correlation with growth in northern Sweden, should be considered in the selective breeding programs.

8) Provenances of Yukon origin had the highest growth but the lowest stiffness at higher latitude, while those of BC origin grew faster at lower latitudes, within a breeding zone. To achieve the highest stiffness for lodgepole pine, provenances of BC origin should be planted at the low-altitude zone (breeding zone five).

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Popular science summary

Trees and their wood products are one of the oldest and the most well-known natural materials used by societies for multiple purposes, including constructing building, making furniture, producing paper and biofuel.

Wood has a wide range of characteristics which determine how well the wood is suited for a particular product. To get the best out of wood, both its quantity and quality should be enhanced through genetic improvement and stand management.

Lodgepole pine has been introduced into Sweden during the mid-1960s. Trees grow fast, they have a good survival and are very productive. However, stem bending and even stem breakage of those trees, which are less resistant to wind, snow-loads, and environmental stresses, have been a major problem in northern Sweden. Additionally, wood produced from such trees is of lower quality for construction purposes, and thus, of lower economical value.

Tree breeding programs aim to enhance the overall value of forest products by applying genetic and economics principles to develop individual trees most suited for the human needs.

In the studies this thesis is based upon, several principles of tree breeding have been applied to quantify the genetic variation and to design the optimal way in order to improve both wood quantity and quality of lodgepole pine in northern Sweden. This will meet the societal need of bio-material for construction and pulp and paper making.

Populärvetenskaplig sammanfattning

Träd och träprodukter är ett av de äldsta och mest kända naturmaterial i vårt samhälle och det används för flera ändamål, bland annat konstruktion av byggnader, tillverkning av möbler, produktion av papper och till biobränsle.

Trä har ett brett register av egenskaper som avgör hur bra träet passar för en viss produkt. För att få ut det mesta av trä, bör både kvantitet och kvalitet förbättras genom genetisk förädling och god skogsskötsel.

Contortatall introducerades i Sverige under mitten av 1960-talet. Trädslaget växer snabbt, har hög överlevnad och är väldigt produktiv. Emellertid har stamböjar och även stambrott av de träd som är mindre motståndskraftiga mot vind, snöbelastning och annan miljöbelastning varit ett stort problem i norra Sverige. Dessutom är trä som från contortatall av lägre kvalitet för byggnadsändamål och därmed av lägre ekonomiskt värde.

Förädling av skogsträd syftar till att förbättra det generella värdet av skogsprodukter. Genom att tillämpa genetiska och ekonomiska principer kan man genetiskt förädla de individer som är mest lämpade för människans behov.

I studierna som denna avhandling är baserad på har flera principer för skogsträdsförädling applicerats för att kvantifiera den genetiska variationen och för att utforma det optimala sättet för att öka produktionen och förbättra kvalitén hos contortatall i norra Sverige. Detta kan möta samhällets behov av biomaterial, konstruktionsvirke och massa- och papperstillverkning.

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