Quantitative Genetics of Wood Quality Traits in Scots Pine

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Cover: Scots pine progeny test, felled logs and sawn boards
    (photo: Irena Fundová)

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Abstract

Wood quality of commercial tree species is important for many wood processing industries and thus should be considered for inclusion in forest tree improvement programs. This thesis evaluated the suitability of various proxy methods for rapid and non-destructive assessment of wood quality traits on standing trees of Scots pine and the potential for genetic improvement of different wood quality traits through recurrent selective breeding.

Penetrometer Pilodyn and micro-drill Resistograph were tested for non-destructive assessment of wood density (DEN$_{PIL}$ and DEN$_{RES}$, respectively), using SilviScan density (DEN$_{SILV}$) as a benchmark. A strong additive genetic correlation was observed between DEN$_{SILV}$ and DEN$_{RES}$ ($r_A = 0.96$), whilst the correlation with DEN$_{PIL}$ was substantially lower ($r_A = 0.74$). Furthermore, SilviScan stiffness (MOE$_{SILV}$) was used as a benchmark for evaluation of several approaches of calculating the dynamic modulus of elasticity (MOE) from standing-tree acoustic velocity (VEL$_{TREE}$). The combination of VEL$_{TREE}$ and adjusted DEN$_{RES}$ provided the most accurate estimate of MOE$_{TREE}$ ($r_A = 0.91$). Additionally, non-destructive acoustic sensing tools were tested at different stages of wood processing (on standing trees, felled logs and sawn boards) using destructively measured sawn-board stiffness (static modulus of elasticity, MOE$_S$) and strength (modulus of rupture, MOR) as benchmarks. They proved to be capable of accurately predicting MOE$_S$ ($r_A \approx 0.8$) while VEL$_{TREE}$, adjusted DEN$_{RES}$ and MOE$_{TREE}$ well reflected MOR ($r_A \approx 0.9$). Genetic variation of shape stability of sawn boards (bow, crook and twist) was also investigated. Under-bark grain angle (GRA) was found to be a good predictor of sawn-board twisting and crooking ($r_A = 0.84$ and 0.62, respectively). The chemical composition of juvenile wood (proportion of cellulose, hemicelluloses, lignin and extractives) was predicted from Fourier transform infrared (FTIR) spectra using partial least squares regression (PLSR) modeling. Individual-tree narrow-sense heritabilities (h_i^2) for all of the studied wood quality traits varied from low to moderate.

Genetic improvement of sawn-board DEN, MOE$_S$ and MOR as the target traits could be achieved through selective breeding for MOE$_{TREE}$, DEN$_{RES}$, stem straightness (STR) or GRA. Selection focusing on GRA would also result in lower bow, crook and twist. Despite the negative genetic correlations between growth and wood quality traits, a possibility of their simultaneous improvement was identified. An index combining stem diameter (DBH) and MOE$_{TREE}$ provided the best compromise.

Keywords: Density, stiffness, strength, shape stability, chemical composition, non-destructive testing, genetic correlation, heritability, breeding, genetic improvement.

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Dedication

To my daughters Lucie and Monika

Contents

List of publications

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

I **Irena Fundová**, Tomáš Funda, Harry X. Wu[*] (2018). Non-destructive wood density assessment of Scots pine (*Pinus sylvestris* L.) using Resistograph and Pilodyn. *PLoS ONE* 13 (9). doi: 10.1371/journal.pone. 0204518.

II **Irena Fundová**, Tomáš Funda, Harry X. Wu[*] (2019). Non-destructive assessment of wood stiffness in Scots pine (*Pinus sylvestris* L.) and its use in forest tree improvement. *Forests* 10, 491, doi: 10.3390/f10060491.

III **Irena Fundová**[*], Henrik R. Hallingbäck, Gunnar Jansson, Harry X. Wu[*] (2020). Genetic improvement of sawn-board stiffness and strength in Scots pine (*Pinus sylvestris* L.). *Sensors* 20 (4): 1129. doi: 10.3390/s20041129.

IV **Irena Fundová**, Henrik R. Hallingbäck, Gunnar Jansson, Harry X. Wu[*]. Genetic improvement of sawn-board shape stability in Scots pine (*Pinus sylvestris* L.) (submitted manuscript).

V Tomáš Funda, **Irena Fundová**, András Gorzsás, Anders Fries, Harry X. Wu[*] (2020). Predicting the chemical composition of juvenile and mature woods in Scots pine (*Pinus sylvestris* L.) using FTIR spectroscopy. *Wood Science and Technology* 54 (2): 289-311. doi:10.1007/s00226-020-01159-4.

VI Tomáš Funda, **Irena Fundová**, Anders Fries, Harry X. Wu[*]. Genetic improvement of the chemical composition of Scots pine (*Pinus sylvestris* L.) juvenile wood for bioenergy production (manuscript).

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The contribution of Irena Fundová to the papers included in this thesis was as follows:

I   Irena Fundová conceived, acquired funding for and designed the project. She was involved in the field sampling. She analysed the data, wrote the first draft of the manuscript, revised the manuscript together with her co-authors and submitted it for publication.

II   Irena Fundová formulated the objectives, performed data analyses, interpreted the results and wrote the first draft of the manuscript. In collaboration with her co-authors, she revised the manuscript and submitted it for publication.

III   Irena Fundová was involved in conceiving and designing the project as well as in acquiring necessary funding for it. She actively participated in all stages of the measurements. She analysed the data, wrote the manuscript in collaboration with her co-authors and submitted it for publication.

IV   Irena Fundová was involved in designing and planning the project. With help of her colleagues, she performed field measurements. She analysed the data, wrote the manuscript and submitted it for publication.

V   Irena Fundová was involved in field sampling and laboratory sample preparation as well as in FTIR spectroscopic analyses. She contributed to the development of predictive models and preparation of the manuscript.

VI   Irena Fundová was involved in defining the objectives and conducting field sampling and laboratory work. She also participated in data preparation and analyses, interpretation of results and writing the manuscript.

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Abbreviations

All abbreviations are explained as they first appear in the text. All studied traits are summarized in Tables 2–7.

1   Introduction

1.1 Scots pine and its breeding in Sweden

Scots pine (*Pinus sylvestris* L.) is a conifer species with the widest natural distribution and the largest ecological amplitude among tree species. It grows in most of Eurasia; from the Atlantic Ocean, over all Europe and Siberia, almost up to the Pacific Ocean, and from beyond the Arctic Circle in Scandinavia to the Mediterranean (Figure 1). Its altitudinal distribution ranges from sea level to about 2,600 meters (Musil, 2003). It grows on a wide variety of soil types (Steven & Carlisle, 1959); however, it is usually outcompeted by other species on more favourable sites (Ellenberg, 1988).

Scots pine, along with Norway spruce (*Picea abies* (L.) H. Karst.), is the most commercially important tree species in Sweden, representing around 40% of the total standing volume (Skogsdata, 2019). Its wood is mainly used for production of construction timber, pulp, paper and furniture (Krakau *et al.*, 2013).

In order to improve trees to better suit industrial requirements, a breeding program for Scots pine in Sweden was launched in 1950s (Werner, 2010; Andersson *et al.*, 2003). Initially, phenotypically superior plus trees were selected in mature natural stands and their grafts were used to establish seed orchards. These plus-trees gave rise to full-sib progeny tests planted in 1970s. To increase the size of the base breeding population, a second round of selection was initiated in 1980s, this time in even-aged planted stands (Danell, 1991).

The current selected base population consists of six thousand plus-trees, selected with the aim of improving survival rate, stem volume, stem straightness and branch characteristics. The breeding population counts more than twelve hundred parents and is divided into 24 subpopulations based on photoperiod and temperature. In order to maintain a sufficient level of genetic diversity, at

least 50 founders were selected for each sub-population (Wilhelmsson & Andersson, 1993).

The rotation period of Scots pine growing in Sweden is long (70–120 years) (Jansson, 2007) and the time between selection and the actual industrial utilization of its wood is even longer. Therefore, objectives of the ongoing breeding program need to be reviewed so that new industrial products as well as changing climate conditions are taken into account (Andersson *et al.*, 2011). In particular, wood quality traits should be incorporated since they affect the quality of many end-products and negatively correlate with the prioritized growth traits (Hong *et al.*, 2014; Fries, 2012).

For that purpose, reliable tools for non-destructive wood quality assessment on standing trees as well as the knowledge of the genetic parameters and relationships between traits are required. Studies underlying this thesis evaluated different non-destructive tools and approaches for the estimation of important wood quality traits in the forest tree breeding context.

Figure 1. Natural distribution of Scots pine. Letter "E" on the map denotes reintroduced populations (Wikimedia, 2017).

1.2 Wood quality

Wood quality represents a combination of physical and chemical properties of wood that enables to satisfy end-product requirements (Barnett & Jeronimidis, 2003). It can be viewed from different perspectives: while it means straight stems with large volumes for forest growers, it is stiffness, strength and dimensional stability for construction industry, fibre length and relative content of cellulose for papermaking industry or relative content of six-carbon sugars for bioethanol production.

1.2.1 Wood density

Wood density is often regarded as the best single predictor of wood quality (Zobel & Jett, 1995; Zobel & Van Buijtenen, 1989). Wood with higher density is more suitable for construction timber (Armstrong *et al.*, 1984), has better machinability (Hernández *et al.*, 2001) and results in greater pulp yield (Ivković & Koshy, 2002). On the other hand, wood with lower density contains more easily collapsible fibres that bond better (Jozsa & Middleton, 1994) and its manipulation is less labour demanding as it is lighter (Perstorper *et al.*, 1995).

Wood density can be estimated using the traditional volumetric method as a mass over volume (Glass & Zelinka, 2010) or from x-ray absorption (Isik & Li, 2003). However, although these methods are very accurate, they are costly and laborious and, since they require at least increment cores to be extracted from tree stems, they cannot be regarded as truly non-destructive.

Penetrometer Pilodyn and micro-drill resistograph have been tested as non-destructive alternatives for wood density assessment of standing trees. Pilodyn measures wood density based on penetration depth of a spring-loaded pin that is shot into the wood (Cown, 1978). Strong genetic correlations of Pilodyn's measurements with wood density were reported for some conifer species (e.g., Desponts *et al.*, 2017; Chen *et al.*, 2015; Fukatsu *et al.*, 2011; Yanchuk & Kiss, 1993); however, the main drawbacks of this tool are shallow penetration (2–3 cm), low sensitivity and the necessity of bark removal when it is thick (Cown, 1978). By contrast, resistograph accounts for the whole stem's profile. It measures energy consumption needed for a slender drilling needle to penetrate bark to bark at a constant speed (Rinn *et al.*, 1996). The drilling profile displays density variation within a stem so that individual growth rings, pith and bark become apparent. The presence of decay or cavities can also be revealed. Nevertheless, an increasing trend of the profiles generated by accumulated needle friction makes the resistograph's practical utilization a little complicated (Rinn, 2012), as an adjustment is needed to eliminate bias in wood density estimates (Isik & Li, 2003). In spite of that, strong genetic correlations between mean resistograph values and wood density were obtained (e.g., El-Kassaby *et al.*, 2011; Bouffier *et al.*, 2008; Isik & Li, 2003).

1.2.2 Wood stiffness

Wood stiffness is an important structural wood quality trait that predetermines the suitability of wood for construction purposes. It is expressed as the modulus of elasticity (MOE) and refers to the pressure an object can be exposed to without becoming permanently deformed (Kretschmann, 2010).

Direct measurement of stiffness (static modulus of elasticity, MOE$_S$) via destructive bending stress testing results in sample destruction and is therefore not suitable for tree breeding or other practical utilization. Acoustic sensing technology that lies in measuring the propagation velocity of acoustic waves appears to be a suitable non-destructive alternative to the destructive testing. In that case, indirect estimate of stiffness (dynamic modulus of elasticity, MOE$_d$) is calculated as squared acoustic velocity multiplied by wood density (Bucur, 2006). The acoustic velocity can be obtained either from (1) time of flight (TOF) or (2) acoustic resonance (AR) (Figure 2). The former approach is suitable for non-destructive estimation of wood stiffness on standing trees. It is based on measuring the time of flight of a stress wave induced by a mechanical force between two probes hammered into a stem. Knowing the distance between the probes, acoustic velocity can be calculated as distance over time. The latter approach is more appropriate for felled logs and sawn boards as it requires cut ends to serve as acoustic wave reflectors so that longitudinal stress waves, generated by a hammer tap, reverberate within a log or board. Acoustic velocity is calculated as two times the first resonance frequency multiplied by the length of a log/board.
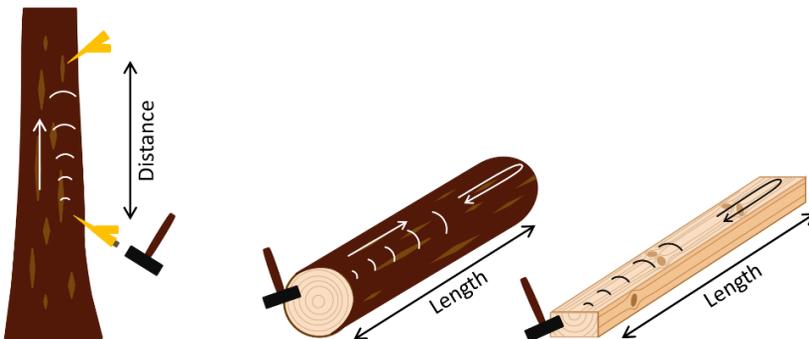
Figure 2. Schema of acoustic velocity measurements on standing trees, felled logs and sawn boards.

The AR approach is considered to be more accurate than TOF (Legg & Bradley, 2016). The effective propagation distance is many times the length of a log/board in AR, as the acoustic waves repeatedly travel forth and back between the cut ends, whilst it is only around one meter for TOF, which may cause a higher sensitivity to local variation in wood properties. Moreover, TOF measurements are limited to a column of outerwood only, whilst AR accounts for the whole log/board's profile (Auty & Achim, 2008; Chauhan & Walker, 2006; Lindström *et al.*, 2004). TOF was also reported to produce higher acoustic velocities than AR (Auty & Achim, 2008; Wang *et al.*, 2007a; Wang *et al.*, 2007b;

Grabianowski *et al.*, 2006; Ross & Wang, 2005), which is in congruence with the findings that longitudinal stiffness increases from pith to bark (Hong *et al.*, 2015; Mora *et al.*, 2009; Chauhan & Walker, 2006). Besides, in the case of logs, the presence of bark causes a lower resonance velocity because bark increases the cross-sectional area but not wood stiffness (Lasserre *et al.*, 2007; Grabianowski *et al.*, 2006). Nevertheless, strong correlations between acoustic velocities estimated using AR and TOF approaches were reported (Baar *et al.*, 2012; Mora *et al.*, 2009; Wang *et al.*, 2007a; Grabianowski *et al.*, 2006).

1.2.3 Shape stability of sawn boards

Shape stability represents one of the crucial sawn-board quality features. Warping, mainly twist, crook and bow (Figure 3) of sawn boards often causes severe problems in the construction industry that can result in prioritizing other engineering materials over wood (Johansson *et al.*, 1994). Among the various forms of warp, twist is considered to be the most undesired one.
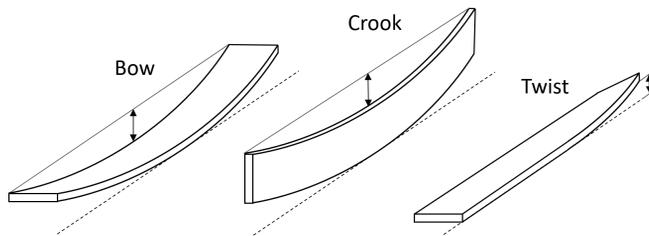
Figure 3. Depiction of sawn board warping.

Shape stability defects are among those traits that do not get expressed until wood is processed. Fortunately, a link between grain angle and board twisting was revealed (e.g., Högberg *et al.*, 2010; Hallingbäck *et al.*, 2008). Grain angle, i.e. spiral grain, refers to the degree of helical deviation from longitudinal arrangement of wood fibres. In northern hemisphere, mature conifer trees usually display right-handed (Z-pattern) grain, while left-handed (S-pattern) grain is more typical for younger trees (Figure 4) (Harris, 1989). It can be measured non-destructively with a wedge grain angle gauge hammered into a stem of a standing tree (Hannrup *et al.*, 2003). For every tree, measurements from two opposite sides have to be combined in order to reduce bias caused by stem leaning (Hansen & Roulund, 1998; Harris, 1984). One should also consider removing a patch of bark prior to the measurement.
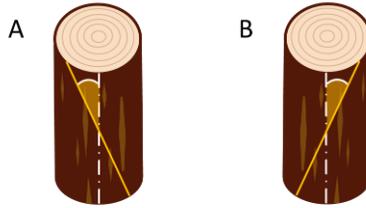
Figure 4. Left-handed (A) and right-handed (B) grain angle.

1.2.4 Fibre traits

Dimensions of fibres (i.e. longitudinal tracheids) are important for pulp and paper industry as they influence properties of final products. Fibre traits such as fibre coarseness, width or wall thickness can be quantified by SilviScan technology (Evans, 1994), whereas microscopic measurements are required to determine fibre length (Chen *et al.*, 2016a).

Microfibril angle, referring to the deviation of cellulose microfibrils in the S2 layer of the secondary cell wall from the long axis of cell, is the main determinant of the mechanical properties of wood (Cave & Walker, 1994). It affects shrinkage during wood drying (Harris & Meylan, 1965) as well as paper properties (Donaldson, 2007). Microfibril angle can be measured by SilviScan using x-ray diffraction (Evans & Ilic, 2001).

1.2.5 Chemical composition of wood

The main chemical components of wood fibres are lignin, cellulose, hemicelluloses and extractives (Figure 5), of which cellulose and hemicelluloses are the most economically important ones (Molinder & Almqvist, 2018).
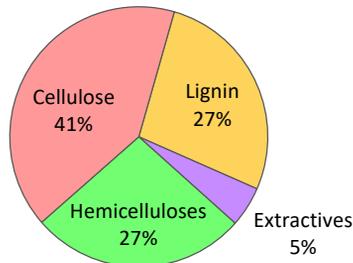
Figure 5. Proportions of main chemical components within Scots pine stem wood (Räisänen & Athanassiadis, 2013).

Cellulose, composed of a linear chain of D-glucose, is essential for pulp and paper industry. Together with six-carbon sugars in hemicelluloses, it is also used

for bioethanol production (Wegner *et al.*, 2010). Although lignin and extractives are often burned as a waste from pulp production, they have a potential for production of fuel, adhesives or chemical feedstock (Kumar *et al.*, 2020; Molinder & Almqvist, 2018; El Mansouri *et al.*, 2007). Extractives also provide wood with its natural durability, as most of these compounds are toxic to fungi and insects (Hillis, 1987).

Expensive and laborious determination of wood chemical composition under laboratory conditions can be replaced with high-throughput vibrational spectroscopy-based techniques, such as near-infrared (NIR) (Tsuchikawa & Kobori, 2015), Fourier-transform infrared (FTIR) (Rodriguez-Saona & Allendorf, 2011), or Raman (Gardiner *et al.*, 1989) spectroscopy. Prediction models, constructed from both wet chemistry and spectral data using a small subset of samples, are applied to spectral profiles of the remaining samples to estimate their chemical compositions (Cozzolino, 2014). Principal component regression (PCR) and partial least squares regression (PLSR) are the most widely used statistical methods in this context (Zhou *et al.*, 2015).

1.3 Quantitative genetics

The majority of traits of forest tree breeding interest are quantitative traits, i.e. traits with continuous distribution (White *et al.*, 2007). Observable phenotypic value of a quantitative trait is governed by a large number of genes, each of which has a very small effect on the phenotype (genotypic variance), and by environmental factors (Nelson *et al.*, 2013). Genotypic variance can be partitioned into additive and non-additive components, the latter of which includes dominance (allelic interactions within loci) and epistasis (allelic interactions between loci). Additive genetic variance arising from additive effects of genes is the main source of resemblance among relatives and determines the magnitude of the response to selection (Falconer & Mackay, 1996). Many forest tree breeding programs are based on the accumulation of additive effects over generations (Berlin *et al.*, 2019).

Most wood quality traits can be genetically improved (reviewed by Wu *et al.*, 2008); considerable genetic variations and moderate to high narrow-sense heritabilities were reported for wood density (e.g., Ukrainetz *et al.*, 2008; Fries & Ericsson, 2006; Louzada & Fonseca, 2002), stiffness (e.g., Chen *et al.*, 2015; El-Kassaby *et al.*, 2011; Kumar *et al.*, 2002), sawn-board twist (Högberg *et al.*, 2014), grain angle (e.g., Hallingbäck *et al.*, 2010; Gapare *et al.*, 2007; Hansen & Roulund, 1998), fibre traits (Chen *et al.*, 2016a; Fries, 2012), microfibril angle (Hayatgheibi *et al.*, 2017; Baltunis *et al.*, 2007), and the proportion of lignin, cellulose (Porth *et al.*, 2013; Pot *et al.*, 2002), hemicelluloses (Porth *et al.*, 2013)

and extractives (Partanen *et al.*, 2011; Fries *et al.*, 2000). By contrast, a low heritability for sawn-board bow and the absence of genetic variation for sawn-board crook were observed by Högberg *et al.* (2014).

The knowledge of genetic correlations among pairs of traits is very important in forest tree breeding since selection for one trait may influence other traits (White *et al.*, 2007). Simultaneous improvement of unfavorably correlated traits, such as stem diameter and wood density (Hong *et al.*, 2014; Fries, 2012; Li & Wu, 2005; Zhang & Morgenstern, 1995), is challenging but possible if appropriate selection indices (Wu & Sanchez, 2011; Cotterill & Dean, 1990) or breeding strategies (Hallingbäck *et al.*, 2014) are applied.

2 Objectives

This thesis is a compilation of quantitative genetic studies focusing on various wood quality traits that are important for construction, pulp & paper and bioenergy industries. The main objectives were to evaluate the suitability of different proxy methods for rapid and non-destructive assessment of wood quality traits on Scots pine standing trees. Genetic parameters for important wood quality traits were estimated and the possibility of incorporating them into a Scots pine breeding program was evaluated. The specific tasks were to:

1. Develop an algorithm to determine mean wood density from a resistograph's drilling profile (**I**).

2. Evaluate methods for non-destructive assessment of wood density (**I**) and wood stiffness (**II** and **III**).

3. Develop partial least squares regression (PLSR) models for predicting the chemical composition of Scots pine juvenile and mature wood from Fourier-transform infrared (FTIR) spectra (**V**).

4. Estimate the genetic variation and heritability of wood quality traits (**I**, **II**, **III**, **IV** and **VI**).

5. Explore phenotypic and additive genetic correlations among growth and wood quality traits (**I**, **II**, **III**, **IV** and **VI**).

6. Investigate the extent to which economically important wood quality traits may be improved by selective breeding (**I**, **II**, **III**, **IV** and **VI**).

3 Materials and Methods

3.1 Field trials

Scots pine full-sib progeny trials selected for studies included in this thesis are located in central and northern Sweden (Figure 6). Grundtjärn (**I & II**), Skorped (**V & VI**) and Vännäsby (**V & VI**) trials were established in 1971, 1972 and 1973, respectively, using completely randomized single-tree plots with ~ 200 post-blocks. Älvkarleby trial (**III & IV**) was established in 1979 following a randomized complete block design with eight blocks; however, one of the blocks was excluded due to excessive mortality. Measurements from Grundtjärn and Älvkarleby were analysed independently whilst those from Skorped and Vännäsby were also subjected to multisite analysis as the included families overlapped. More details about the trials are provided in Table 1.

Figure 6. Locations of Scots pine progeny trials included in this thesis.

Table 1. *Details of progeny trials included in this thesis.*

Progeny trial	Grundtjärn	Älvkarleby	Skorped	Vännäsby
Study	I, II	III, IV	V, VI	V, VI
Site code	S23F 711261	S22F791110E	411-2-H72-Y	411-3-V73-AC
Latitude	63.56° N	60.54° N	63.34° N	64.03° N
Longitude	17.41° E	17.44° E	17.64° E	19.85° E
Altitude (m a.s.l.)	320	25	330	200
Established	1971	1979	1972	1973
Progeny	Full-sib	Full-sib	Full-sib	Full-sib
Number of families	179	90	202	204
Number of parents	45	24	70	50
Design	CRST	RCB	CRST	CRST
Number of blocks / post-blocks[1]	181[1]	7	210[1]	208[1]
Spacing (m)	2.2 × 2.2	2 × 2	2.2 × 2.2	2.2 × 2.2

[1] One post-block contains 4 × 10 trees.
CRST – Completely randomized single-tree plots
RCB – Randomized complete block design

3.2 Studied traits

3.2.1 Growth traits

Assessed growth traits are summarized in Table 2. Diameter at breast height (DBH) and height (HGT) were measured on standing trees. DBH, an easy-to-measure growth trait, was included in all quantitative genetic studies. Stem volume (VOL) was calculated as a function of height and diameter (Brandel, 1990):

$$VOL = \exp[-2.7841 + 1.9474 \cdot ln(DBH) - 0.05947 \cdot ln(DBH + 20) + 1.40958 \cdot ln(HGT) - 0.4581 \cdot \ln(HGT - 1.3)]. \tag{1.}$$

Stem straightness (STR) was visually scored using a 9-point scale, where 1 and 9 represent extremely crooked and very straight stems, respectively.

Table 2. *Summary of growth traits.*

Trait description	Units	Abbreviation	Study	Sample
Diameter at breast height	cm	DBH	I, II, III, IV, VI	Tree
Height	m	HGT	I, II, VI	Tree
Stem volume (Eq. 1)	dm^3	VOL	I, II, VI	Tree
Stem straightness (9-point scale)	–	STR	III, IV	Tree

3.2.2 Wood density

Several different methods of wood density assessment were employed (Table 3). The traditional volumetric method (DEN$_{VOL}$), estimating density as mass over volume, was applied on sawn boards produced in Studies **III** and **IV**. Wood density estimated based on x-ray absorption using SilviScan technology (CSIRO, Australia) (DEN$_{SILV}$) was used in Studies **I** and **II**. For that purpose, 10-mm pith-to-bark increment cores were extracted from standing trees, ca 1.3 m above ground, and cut into thin strips.

Non-destructive assessment of wood density on standing trees was carried out using the micro-drill Resistograph IML-RESI PD300 (Instrumenta Mechanic Labor, Germany) and penetrometer Pilodyn 6J Forest (PROCEQ, Switzerland). Trees were drilled with resistograph (**I**, **II**, **III**, **IV** and **VI**) bark-to-bark and shot with Pilodyn (**I** and **II**) through bark (DEN$_{PIL}$) and after removing a patch of bark (DEN$_{PIL.B}$) ca 1.3 m above ground. Measurements were performed with an effort to avoid branches, knots and compression wood.

Resistograph's drilling profiles (resistograms) were adjusted (detrended and debarked) in order to eliminate increasing trend caused by accumulated needle friction and to obtain more accurate wood density estimates (Figure 7) (Fundova *et al.*, 2018). Resistograph wood density (DEN$_{RES}$) was calculated as an arithmetic mean of all density numbers along a profile, divided by four for better scaling.
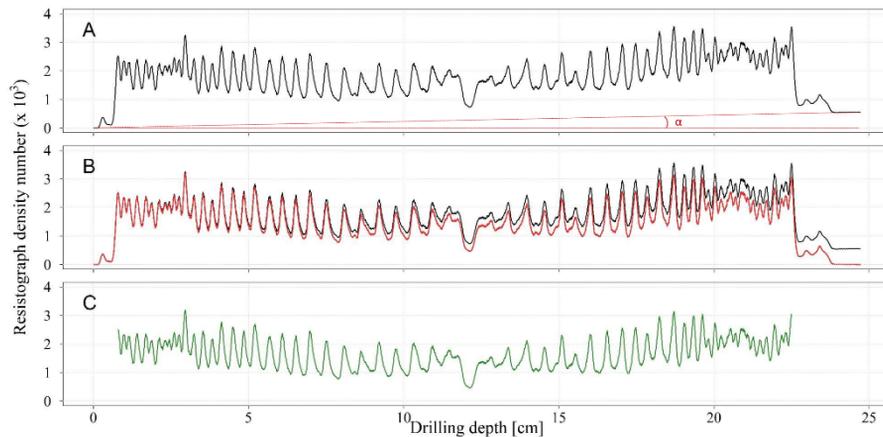
Figure 7. Unadjusted (A), detrended (B), and detrended & debarked (C) resistograms.

Table 3. *Summary of wood density traits.*

Trait description	Units	Abbreviation[†]	Study	Sample
Volumetric density	kg·m^{-3}	DEN$_{VOL}$	III	Board
		DEN$_{BOARD}$	IV	
SilviScan mean wood density	kg·m^{-3}	DEN	I	Core
		DEN$_{SILV}$	II	
SilviScan density of earlywood	kg·m^{-3}	EWD	I, II	Core
SilviScan density of transition wood	kg·m^{-3}	TWD	I, II	Core
SilviScan density of latewood	kg·m^{-3}	LWD	I, II	Core
Unadjusted resistograph mean density number	–	RES[*]	I	Tree
		DEN$_{RES}$[*]	II	
Adjusted resistograph mean density number	–	RES$_{TB}$	I	Tree
(detrended and debarked)		DEN$_{RES.TB}$	II	
		DEN$_{RES}$[*]	III	
		DEN$_{TREE}$	IV	
		RES[*]	VI	
Depth of Pilodyn pin penetration with bark	mm	PIL	I	Tree
		DEN$_{PIL}$	II	
Depth of Pilodyn pin penetration without bark	mm	PIL$_B$	I	Tree
		DEN$_{PIL.B}$	II	

[†] Different abbreviations were used for the same trait across studies.

[*] The same abbreviations was used for different traits across studies.

3.2.3 Wood stiffness, strength and acoustic velocity

Destructive measurements of wood stiffness and strength were carried out on air-dried 50 × 100 × 3000 mm sawn boards (**III** and **IV**). A four-point bending test was performed according to EN 408 standard (Figure 8) (CEN, 2010b) so that the weakest point, detected by WoodEye scanner (WoodEye AB, Sweden) (Olsson *et al.*, 2013), could be placed in the centre. Local (MOE$_{S.local}$) and global (MOE$_{S.global}$) moduli of elasticity and modulus of rupture (MOR) were calculated following Equations 2, 3 and 4, respectively. For MOE$_S$, moisture content was adjusted to 12% according to EN 384 (CEN, 2010a).

$$MOE_{S.local} = \frac{3al_1^2 F}{4bh^3 w} \tag{2.}$$

$$MOE_{S.global} = \frac{l^3 F}{bh^3 y}\left[\frac{3a}{4l} - \left(\frac{a}{l}\right)^3\right] \tag{3.}$$

$$MOR = \frac{3aF_{max}}{bh^2} \tag{4.}$$

where F is an increment of applied load, F_{max} is maximum load, b is board thickness, h is board width, a is distance between loading and the nearest bearing point, l is total distance between bearing points, l_1 is length of central gauge, and w and y are local and global deformation increments, respectively.
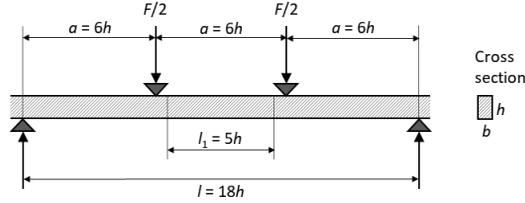
Figure 8. Schema of four-point bending test. F is load increment, a is distance between load points, l_1 is central gauge length, l is test span, h is board width and b is board thickness.

SilviScan wood stiffness (MOE_{SILV}), derived from x-ray absorption and diffraction of thin pith-to-bark wood strips (Evans & Ilic, 2001), was used in Study **II**.

In Studies **II**, **III**, **IV** and **VI**, acoustic sensing technology was applied with the aim of non-destructively assessing wood stiffness either on standing trees, felled logs or saw-boards. Dynamic modulus of elasticity (MOE_d) was estimated from acoustic velocity (VEL) and wood density (DEN) (Bucur, 2006):

$$MOE_d = VEL^2 \cdot DEN. \tag{5.}$$

Standing-tree acoustic velocity (VEL_{TREE}) was recorded between two probes, hammered into a stem ca one meter apart, using Hitman ST300 (Fiber-gen, New Zealand). VEL_{TREE} and adjusted DEN_{RES} measured on standing trees were supplied to Equation 5 to obtain an estimate of standing-tree modulus of elasticity (MOE_{TREE}). In Study **II**, VEL_{TREE} was combined in Equation 5 with several other wood density estimates such as unadjusted DEN_{RES}, DEN_{SILV}, DEN_{PIL}, $DEN_{PIL.B}$ and constant density (Table 4) to evaluate various approaches for standing-tree MOE_d estimation (Fundova *et al.*, 2019).

On felled logs, acoustic velocity (VEL_{LOG}) was calculated as

$$VEL = 2Lf \tag{6.}$$

where L is length of a log and f is resonance frequency. Resonance frequency, induced by tapping a log with a hammer in the longitudinal direction, was recorded by Android application Resonance Log Grader (Fakopp Enterprise Bt., Hungary). Following Equation 5, dynamic modulus of elasticity of logs (MOE_{LOG}) was estimated from VEL_{LOG} and adjusted DEN_{RES} (**III**, **IV**).

MTG timber grader (Brookhuis MicroElectronics, Netherlands) was used for measuring acoustic resonance to determine sawn-board acoustic velocity

(VEL$_{BOARD}$). Resonance frequency (f) of an impulse, generated by an integrated electric hammer, was recorded and sawn-board acoustic velocity was calculated following Equation 6. For the estimation of sawn-board dynamic modulus of elasticity (MOE$_{BOARD}$), VEL$_{BOARD}$ and DEN$_{VOL}$ were supplied to Equation 5.

Table 4. *Summary of wood stiffness, strength and acoustic velocity traits.*

Trait description	Unit	Abbreviation[†]	Study	Sample
Acoustic velocity				
Acoustic velocity measured by Hitman	km·s⁻¹	VEL	II, VI	Tree
		VEL$_{HIT}$	III	
		VEL$_{TREE}$	IV	
Acoustic velocity measured by Fakopp (Eq. 6)	km·s⁻¹	VEL$_{FAK}$	III	Log
		VEL$_{LOG}$	IV	
Acoustic velocity measured by MTG timber grader (Eq. 6)	km·s⁻¹	VEL$_{MTG}$	III	Board
		VEL$_{BOARD}$	IV	
Wood stiffness				
Local static modulus of elasticity (Eq. 2)	GPa	MOE$_{S.local}$	III, IV	Board
Global static modulus of elasticity (Eq. 3)	GPa	MOE$_{S.global}$	III, IV	Board
SilviScan modulus of elasticity	GPa	MOE$_{SILV}$	II	Core
Dynamic modulus of elasticity calculated from VEL$_{HIT}$ and a constant density of 1,000 kg·m⁻³ (Eq. 5)	GPa	MOE$_{DEN_{CONST}}$	II	Tree
Dynamic modulus of elasticity calculated from VEL$_{HIT}$ and DEN$_{SILV}$ (Eq. 5)	GPa	MOE$_{DEN_{SILV}}$	II	Tree
Dynamic modulus of elasticity calculated from VEL$_{HIT}$ and unadjusted DEN$_{RES}$ (Eq. 5)	GPa	MOE$_{DEN_{RES}}$	II	Tree
Dynamic modulus of elasticity calculated from VEL$_{HIT}$ and adjusted DEN$_{RES}$ (Eq. 5)	GPa	MOE$_{DEN_{RES.TB}}$	II	Tree
		MOE$_{TREE}$	III, IV	
		MOE$_d$	VI	
Dynamic modulus of elasticity calculated from VEL$_{HIT}$ and DEN$_{PIL}$ (Eq. 5)	GPa	MOE$_{DEN_{PIL}}$	II	Tree
Dynamic modulus of elasticity calculated from VEL$_{HIT}$ and DEN$_{PIL.B}$ (Eq. 5)	GPa	MOE$_{DEN_{PIL.B}}$	II	Tree
Dynamic modulus of elasticity calculated from VEL$_{FAK}$ and adjusted DEN$_{RES}$ (Eq. 5)	GPa	MOE$_{LOG}$	III, IV	Log
Dynamic modulus of elasticity calculated from VEL$_{MTG}$ and DEN$_{VOL}$ (Eq. 5)	GPa	MOE$_{BOARD}$	III, IV	Board
Wood strength				
Modulus of rupture (Eq. 4)	MPa	MOR	III, IV	Board

[†] Different abbreviations were used for the same trait across studies.

3.2.4 Shape stability traits and grain angle under bark

Shape stability traits, namely bow, crook and twist of air-dried sawn boards, were assessed in Study **IV** (Figure 3, Table 5). Measurements were carried out on a right-angled flat table using a wedge with a millimetre scale. Bow (BOW) and crook (CRK) were measured as the maximum warp on a board's face and along a board's edge, respectively. Twist (TWI) was measured as a deviation of the top corner from the surface, while bottom end of the board was fixed. The direction of warping was taken into account by assigning positive and negative signs according to Mishiro and Booker (1988).

Grain angle (GRA) was measured under bark on standing trees using a wedge grain angle gauge (Chalmers Institute of Technology, Sweden), gently hammered into a stem at breast height (Hannrup *et al.*, 2003). A patch of bark was removed prior to each measurement. Measurements from two opposite sides (northern and southern) were combined to reduce bias caused by stem leaning (Hansen & Roulund, 1998; Harris, 1984). Positive and negative values were assigned to left-handed and right-handed grain, respectively (Hannrup *et al.*, 2003) (Study **IV**).

Table 5. *Summary of shape stability traits and grain angle under bark.*

Trait description	Units	Abbreviation	Study	Sample
Maximum bow	mm	BOW	IV	Board
Maximum crook	mm	CRK	IV	Board
Maximum twist	mm	TWI	IV	Board
Grain angle under bark	°	GRA	IV	Tree

3.2.5 Fibre traits

Fibre traits were estimated using SilviScan technology (Evans, 1994). Microfibril angle (MFA) was determined from x-ray diffraction, whereas fibre width in radial (FRW) and tangential (FTW) directions from image analysis. Fibre coarseness (FCS) was calculated from DEN_{SILV}, FRW and FTW and fibre wall thickness (FWT) from DEN_{SILV}, FRW, FTW and fibre wall density (Table 6, Studies **I** and **II**).

Table 6. *Summary of fibre traits.*

Trait description	Units	Abbreviation	Study	Sample
Microfibril angle	°	MFA	I, II	Core
Fibre wall thickness	μm	FWT	I, II	Core
Fibre coarseness	μg·m⁻¹	FCS	I, II	Core
Fibre width in radial direction	μm	FRW	I, II	Core
Fibre width in tangential direction	μm	FTW	I, II	Core

3.2.6 Chemical compositional traits

Bark-to-bark 5-mm increment cores were extracted from standing trees at ca 1.3 m above ground. Growth rings 2–6 counted from the pith and 8–12 counted from the bark, corresponding to juvenile (70 samples) and mature (39 samples) wood, respectively, were ground into fine powder using Retsch MM400 bead mil (Retch GmbH, Germany) and were subjected to wet chemistry analyses in MoRe Research (Örnsköldsvik, Sweden) to determine their chemical composition (Study **V**). The content of carbohydrates was quantified following protocol SCAN-CM 71:09 (SCAN, 2009); the monosaccharides glucose, xylose, mannose, galactose and arabinose (GLU, XYL, MAN, GAL and ARA, respectively) were subsequently quantified using ion chromatography (Dionex ICS-5000, Thermo Scientific Inc., USA). The ratio of cellulose (CEL) to hemicelluloses (HEM) was determined using a formula developed by Sjöström (1993). Total lignin (LIG) was quantified as a sum of Klason and acid-soluble lignin following protocols TAPPI (2002) and TAPPI (1991), respectively. The analysis of extractives (EXT) was performed according to protocol SCAN-CM 67:03 (SCAN, 2003).

The same subsets of samples were mixed with potassium bromide (KBr) at a weight ratio of approximately 1:55 and manually ground into fine powder with agate pestle and mortar for subsequent Fourier-transform infrared (FTIR) spectral analyses using vacuum bench spectrometer Bruker IFS 66v/S (Bruker Optics, Germany). Raw FTIR spectra were standardized using an open source interface available at https://www.umu.se. The procedure involved trimming to retain only the "fingerprint" region of 1870–770 cm^{-1}, baseline correction (Eilers, 2004), normalization, and smoothing (Savitzky & Golay, 1964).

Standardized FTIR spectra, along with the chemical composition determined in the wet lab, were subsequently used for the development of partial least squares regression (PLSR) predictive models. The computation was performed in SAS software (PROC PLS) (SAS Institute, 2008) using the non-linear iterative partial least square (NIPALS) algorithm and models were validated with a split-sample cross-validation test. Root mean square error of predictions (*RMSEP*) was used as the criterion for model selection, and the best performing models for juvenile wood in terms of minimized *RMSEP* were then applied for predicting the chemical composition of all 1246 trees included in Study **VI** (Table 7).

Table 7. *Summary of chemical compositional traits.*

Trait description	Units	Abbreviation	Study	Sample
Lignin	%	LIG	V, VI	Core
Cellulose	%	CEL	V, VI	Core
Hemicelluloses	%	HEM	V, VI	Core
Glucose	%	GLU	V, VI	Core
Mannose	%	MAN	V, VI	Core
Xylose	%	XYL	V, VI	Core
Galactose	%	GAL	V, VI	Core
Arabinose	%	ARA	V, VI	Core
Extractives	%	EXT	V, VI	Core

3.3 Statistical analysis

3.3.1 General model

Variance and covariance components were estimated using the statistical package ASReml 4 (Gilmour *et al.*, 2015). Response variables were fitted into univariate and multivariate individual-tree linear mixed models:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \tag{7.}$$

where $\mathbf{y}$ is a vector of measured values, $\mathbf{b}$ is a vector of fixed effects, $\mathbf{u}$ is a vector of random effects and $\mathbf{e}$ is a vector of residuals. $\mathbf{X}$ and $\mathbf{Z}$ are design matrices, linking phenotypic observations to fixed and random effects, respectively.

3.3.2 Heritability, correlations and correlated response to selection

Individual-tree narrow-sense (h_i^2) and broad-sense (H_i^2) heritabilities were estimated as

$$h_i^2 = \frac{\sigma_A^2}{\sigma_P^2} \tag{8.}$$

$$H_i^2 = \frac{\sigma_G^2}{\sigma_P^2} \tag{9.}$$

where σ_A^2, σ_P^2 and σ_G^2 are additive genetic, phenotypic and genotypic variance components, respectively. Phenotypic and additive genetic correlation coefficients (r_{xy}) between pairs of traits (x and y) were calculated as

$$r_{xy} = \frac{\sigma_{xy}}{\sqrt{\sigma_x^2 \times \sigma_y^2}} \tag{10.}$$

where σ_x^2 and σ_y^2 refer to phenotypic or additive genetic variances for traits x and y, respectively, and σ_{xy} is phenotypic or additive genetic covariance between traits x and y. Genetic gain (G_{A_x}) for direct selection was estimated as

$$G_{A_x} = i h_x \sigma_{A_x} \tag{11.}$$

and correlated response (CR_{A_y}) to selection for a target trait y was estimated as

$$CR_{A_y} = i h_x r_{A_{xy}} \sigma_{A_y} \tag{12.}$$

where i is selection intensity, h_x is square root of narrow-sense heritability for trait x, $r_{A_{xy}}$ is additive genetic correlation between traits x and y, and σ_{A_x} and σ_{A_y} are additive genetic standard deviations for traits x and y, respectively (**I**, **II**, **III**, **IV, VI**).

3.3.3 Index selection

In Study **II**, Smith-Hazel selection index (*I*) (Hazel, 1943) was applied in order to explore the possibility of simultaneous improvement of DBH with negatively correlated DEN and MOE:

$$I = b_1 P_1 + b_2 P_2 + \cdots + b_n P_n \tag{13.}$$

where P_1 to P_n represent the phenotypic performance of desired traits and b_1 to b_n refer to their corresponding index coefficients calculated as

$$\mathbf{b} = \mathbf{P}^{-1}\mathbf{Aw} \tag{14.}$$

where **P** and **A** denote phenotypic and additive genetic variance-covariance matrices, respectively, and **w** is vector of weights for each trait. The expected genetic gain (ΔA_x) for trait x included in the Smith-Hazel index was estimated according to Cotterill and Dean (1990) as:

$$\Delta A_x = \frac{i}{\sigma_I} \left(b_x \sigma_{A_x}^2 + b_y \sigma_{A_{xy}} \right) \tag{15.}$$

where i is selection intensity, $\sigma_{A_x}^2$ is additive genetic variance for trait x, $\sigma_{A_{xy}}$ is additive genetic covariance for traits x and y, b_x and b_y are index coefficients for traits x and y, respectively, and σ_I is phenotypic standard deviation of the index derived as

$$\sigma_I = \sqrt{\mathbf{b^T P b}}. \tag{16.}$$

4 Results and Discussion

4.1 Additive genetic variation in studied traits

Descriptive statistics along with coefficients of phenotypic (CV_P) and additive genetic (CV_A) variation is summarized in Table 8. CV_A varied from 1.5% (VEL_TREE, **III**) to 34.5% (EXT, **VI**) and CV_P from 3.7% (FRW, **I**) to 54.9% (EXT, **VI**). Of growth traits, VOL exhibited the highest additive genetic variation (~ 15%) and HGT the lowest (~ 5%), which was observed in Scots pine earlier (Fries, 2012; Kroon *et al.*, 2008; Jansson, 2007). CV_A for density traits averaged ca 6%, which is consistent with other studies on conifer species (Hayatgheibi, 2018; Chen *et al.*, 2015; Fries, 2012; Johnson & Gartner, 2006). Compared to wood density, MOE traits showed mostly higher phenotypic and genetic variations. CV_A ranged from 5.4% to 16.0%; the lowest CV_A values were observed in Study **III**. Values within this range were also reported in other studies (e.g., Chen *et al.*, 2015; Högberg *et al.*, 2014; Steffenrem *et al.*, 2009; Johnson & Gartner, 2006). A rather low CV_A (~ 4%) for VEL traits was in congruence with those obtained by Chen *et al.* (2015) and Johnson and Gartner (2006). Chemical compositional traits exhibited low genetic variation except for GAL and EXT, for which CV_A coefficients were three and seven-fold greater compared to other traits within the group, respectively. Slightly lower CV_A values for some of the chemical traits were observed by Ukrainetz *et al.* (2008) and Pot *et al.* (2002).

4.2 Inheritance of studied traits

Individual-tree narrow-sense heritabilities (h_i^2) are presented in Table 8. Heritabilities for growth traits were low to moderate; the highest ones were obtained for HGT (~ 0.3). The results correspond with the finding of Fries (2012),

whereas weaker heritabilities were reported by Kroon *et al.* (2008), Jansson (2007) and Högberg *et al.* (2010). Genetic control of wood density traits was moderate; the highest heritabilities were observed for DEN_{SILV} and $DEN_{RES.adjusted}$ (0.40–0.46). Heritabilities of the same magnitude were reported in numerous studies (Högberg *et al.*, 2014; Fries, 2012; Steffenrem *et al.*, 2009; Ukrainetz *et al.*, 2008; Wu *et al.*, 2008; Fries & Ericsson, 2006; Hannrup *et al.*, 1998).

Different MOE estimates showed moderate heritabilities (0.37–0.58), except for those in Study **III**, whose genetic control was rather low (0.08–0.26). Earlier published heritabilities for MOE also varied from low (Hallingbäck *et al.*, 2018; Hayatgheibi *et al.*, 2017; Högberg *et al.*, 2014; El-Kassaby *et al.*, 2011) to moderate (Cherry *et al.*, 2008; Matheson *et al.*, 2008; Johnson & Gartner, 2006; Kumar *et al.*, 2002). Similarly, genetic control of VEL was low to moderate, while that of VEL_{TREE} was moderate in Studies **II** and **VI** and very low in Study **III**. Other studies with conifer species mostly reported moderate heritabilities (~ 0.38) for VEL_{TREE} (Walker *et al.*, 2019; Lenz *et al.*, 2010; Cherry *et al.*, 2008; Matheson *et al.*, 2008; Kumar *et al.*, 2002) although lower heritabilities (~ 0.15) were observed as well (Chen *et al.*, 2015; El-Kassaby *et al.*, 2011).

Of shape stability traits (Study **IV**), TWI exhibited the highest genetic control (0.37) whilst CRK the lowest (0.05). Similar heritability for TWI but lower for BOW and completely absent for CRK was reported by Högberg *et al.* (2014). Moderate heritability for GRA (0.40) is in agreement with studies on Scots pine (Högberg *et al.*, 2010; Hannrup *et al.*, 2003) and other conifer species (Högberg *et al.*, 2014; Hallingbäck, 2010; Hallingbäck *et al.*, 2010; Steffenrem *et al.*, 2009; Gaspar *et al.*, 2008; Gapare *et al.*, 2007; Costa e Silva *et al.*, 2000).

Heritabilities of chemical compositional traits (Study **VI**) ranged from 0.23 (GLU) to 0.46 (HEM). Slightly higher estimates for LIG and CEL were reported by Pot *et al.* (2002) whilst lower by Sykes *et al.* (2006). Moderate genetic control of EXT was in congruence with several other studies (Lepoittevin *et al.*, 2011; Zhou *et al.*, 2000; Cown *et al.*, 1992).

Table 8. *Descriptive statistics. Number of observations (n), mean value, coefficient of phenotypic (CV$_P$) and additive genetic (CV$_A$) variation, individual-tree narrow-sense heritability (h$_i^2$) (standard error in parentheses) and study, in which the parameters are presented.*

Trait	n	Mean	CV$_P$	CV$_A$	h$_i^2$	Study
Growth traits						
DBH	622	19.7	16.3	7.6	0.22 (0.07)	I
	1896	17.2	23.8	11.7	0.24 (0.08)	III
	1215	16.0	17.1	5.5	0.10 (0.04)[a]	VI
HGT	622	16.3	8.1	4.8	0.35 (0.09)	I
	1246	10.1	8.9	5.2	0.33 (0.07)[a]	VI
VOL	622	251.4	34.5	16.2	0.22 (0.07)	I
	1215	111.7	37.0	14.8	0.16 (0.05)[a]	VI
STR	1896	7.8	9.9	5.2	0.28 (0.08)	III
Wood density						
DEN$_{VOL}$	494	462.1	6.1	3.6	0.34 (0.11)	III
DEN$_{SILV}$	622	447.9	7.4	5.0	0.46 (0.10)	I
DEN$_{RES}$ unadjusted	622	464.4	8.5	5.0	0.35 (0.10)	I
DEN$_{RES}$ adjusted	622	462.0	9.0	5.9	0.43 (0.11)	I
	1892	521.5	10.3	6.5	0.40 (0.11)	III
	1244	485.6	10.2	6.6	0.42 (0.09)[a]	VI
DEN$_{PIL}$	622	21.7	10.8	6.1	0.32 (0.09)	I
DEN$_{PIL.B}$	622	16.4	11.4	6.4	0.32 (0.09)	I
Wood stiffness						
MOE$_{S.local}$	494	8.5	23.2	7.7	0.11 (0.07)	III
MOE$_{S.global}$	495	7.9	19.1	5.4	0.08 (0.07)	III
MOE$_{SILV}$	622	10.2	18.5	11.6	0.39 (0.09)	I
MOE$_{BOARD}$	495	6.9	19.0	7.8	0.17 (0.08)	III
MOE$_{LOG}$	494	24.3	17.9	9.1	0.26 (0.09)	III
MOE$_{DEN_{CONST}}$	622	14.9	17.7	10.8	0.37 (0.09)	II
MOE$_{DEN_{SILV}}$	622	6.7	21.7	14.7	0.46 (0.10)	II
MOE$_{DEN_{RES.unadjusted}}$	622	7.0	20.7	13.7	0.44 (0.11)	II
MOE$_{DEN_{RES.adjusted}}$*	622	6.9	21.7	14.6	0.45 (0.11)	II
	1873	9.4	19.2	9.0	0.22 (0.08)	III
	613	7.7	21.0	16.0	0.58 (0.13)[b]	VI
MOE$_{DEN_{PIL}}$	622	6.9	22.7	14.4	0.40 (0.10)	II
MOE$_{DEN_{PIL.B}}$	622	9.2	22.8	14.6	0.41 (0.10)	II
Wood strength						
MOR	495	31.8	24.0	9.0	0.14 (0.07)	III

Trait	n	Mean	CV_P	CV_A	h_i^2	Study
Acoustic velocity						
VEL$_{TREE}$	622	3.8	9.0	5.5	0.37 (0.09)	II
	1874	4.2	6.7	1.5	0.05 (0.03)	III
	612	4.0	7.6	5.5	0.53 (0.12)[b]	VI
VEL$_{LOG}$	486	6.75	5.5	2.5	0.20 (0.09)	III
VEL$_{BOARD}$	496	3.88	7.2	3.5	0.24 (0.10)	III
Shape stability traits and under-bark grain angle						
BOW	493	11.37	3.5[†]	1.6[†]	0.21 (0.10)	IV
CRK	495	1.44	3.6[†]	0.8[†]	0.05 (0.05)	IV
TWI	494	9.56	3.3[†]	2.0[†]	0.37 (0.13)	IV
GRA	1891	1.97	1.9[†]	1.2[†]	0.40 (0.11)	IV
Fiber traits						
MFA	615	17.3	23.8	13.0	0.30 (0.08)	I
FWT	617	2.5	7.9	5.8	0.53 (0.11)	I
FCS	618	406.4	8.2	6.2	0.57 (0.11)	I
FRW	616	28.7	3.7	2.5	0.46 (0.10)	I
FTW	619	33.5	4.2	3.1	0.55 (0.11)	I
Chemical compositional traits						
LIG	1246	26.2	9.6	5.5	0.32 (0.07)[a]	VI
CEL	1246	32.0	7.5	3.8	0.25 (0.06)[a]	VI
HEM	1246	22.2	7.5	5.1	0.46 (0.09)[a]	VI
GLU	1246	34.7	7.8	3.8	0.23 (0.06)[a]	VI
MAN	1246	7.9	9.6	4.6	0.24 (0.06)[a]	VI
XYL	1246	5.8	8.1	3.9	0.24 (0.06)[a]	VI
GAL	1245	4.5	30.5	14.8	0.24 (0.07)[a]	VI
ARA	1246	1.7	11.7	6.6	0.32 (0.08)[a]	VI
EXT	1246	9.2	54.9	34.5	0.37 (0.08)[a]	VI

[*] Refers to MOE$_{TREE}$.

[†] Phenotypic (σ_P) and additive genetic (σ_A) standard deviations are shown instead of CV_P and CV_A, respectively.

[a] Estimates from multisite analysis (Skorped and Vännäsby).

[b] Estimates from single-site analysis (Vännäsby only).

4.3 Non-destructive assessment of wood density

In order to find a reliable method for non-destructive wood density assessment of standing trees, penetrometer Pilodyn and micro-drill resistograph were tested using SilviScan x-ray wood density (DEN$_{SILV}$) as a benchmark (Table 9, Study **I**) (Fundova *et al.*, 2018). Since Scots pine trees have thick bark and Pilodyn has shallow penetration depth, it was applied with bark (DEN$_{PIL}$) and

without bark ($DEN_{PIL.B}$) to examine the influence of bark on wood density estimates. Phenotypic correlations of DEN_{SILV} with inverse Pilodyn penetration depth were weak, whereas additive genetic correlations were moderate with DEN_{PIL} (0.59) and strong with $DEN_{PIL.B}$ (0.74). The results were in accordance with Desponts *et al.* (2017) and Sprague *et al.* (1983). A stronger genetic correlation (0.96) was estimated by Chen *et al.* (2015).

Unlike Pilodyn, resistograph considers the whole stem profile, but its resistograms exhibit an increasing trend caused by accumulated needle friction. To obtain more accurate wood density estimates, linear adjustment followed by bark exclusion was proposed in Study **I**. A strong genetic correlation of 0.89 between resistograph density (DEN_{RES}) and the benchmark DEN_{SILV} was observed already with raw data, and an even stronger (0.96) was attained after the adjustment; the effect of the adjustment was more pronounced in phenotypic correlations (from 0.59 to 0.72). Correlations of the same magnitude were reported by Eckard *et al.* (2010) and Bouffier *et al.* (2008).

Table 9. *Additive genetic and phenotypic correlations of benchmark SilviScan wood density with resistograph and Pilodyn density estimates (Study **I**, standard errors in parentheses).*

	Correlation with DEN_{SILV}	
	Genetic	**Phenotypic**
$DEN_{RES.unadjusted}$	0.89 (0.06)	0.59 (0.03)
$DEN_{RES.adjusted}$	0.96 (0.03)	0.72 (0.02)
DEN_{PIL}	0.59 (0.14)	0.38 (0.04)
$DEN_{PIL.B}$	0.74 (0.11)	0.44 (0.03)

4.4 Non-destructive assessment of wood stiffness

Different approaches of calculating the dynamic modulus of elasticity from standing-tree acoustic velocity (VEL_{TREE}) were tested in Study **II** (Fundova *et al.*, 2019) using SilviScan data as a benchmark (MOE_{SILV}, Table 10). $MOE_{DEN_{SILV}}$ combining VEL_{TREE} with DEN_{SILV} provided the best estimate of standing-tree MOE ($r_A = 0.95$ and $r_P = 0.75$), which was in a good accordance with other studies (Chen *et al.*, 2015; Raymond *et al.*, 2007); however, this relationship may be overestimated as DEN_{SILV} was also used for calculating $MOE_{DEN_{SILV}}$. Moreover, x-ray density is not appropriate for large-scale assessment as it is cost, time and labour intensive.

Of the proxies potentially suitable for operational breeding, the best estimate of MOE was, at the genetic level, attained by VEL_{TREE}, $MOE_{DEN_{RES.adjusted}}$, and $MOE_{DEN_{CONST}}$ ($r_A = 0.91$ for all). However, at the phenotypic level, $MOE_{DEN_{RES.adjusted}}$ provided a better estimate ($r_P = 0.70$ compared to $r_P = 0.65$),

which implies that additional information in the form of adjusted resistograph density slightly improved the MOE estimate. Similar genetic and phenotypic correlations of the benchmark MOE_{SILV} with $MOE_{DEN_{CONST}}$ were obtained by Hayatgheibi *et al.* (2017), whereas slightly stronger phenotypic correlations with VEL_{TREE} were observed by Auty and Achim (2008) and El-Kassaby *et al.* (2011).

Wood densities DEN_{PIL}, $DEN_{PIL.B}$ and $DEN_{RES.unadjusted}$ did not appear to be appropriate for the estimation of standing-tree MOE_d in Scots pine (Table 10). Correlations of their MOE_d estimates with the benchmark MOE_{SILV} were the same or lower compared to those of MOE_{SILV} with VEL_{TREE} where no additional wood density information was supplied. By contrast, a very strong genetic correlation between $MOE_{DEN_{PIL}}$ and MOE_{SILV} was observed in Norway spruce (Chen *et al.*, 2015).

Table 10. *Additive genetic and phenotypic correlations of benchmark SilviScan modulus of elasticity with different dynamic moduli of elasticity and acoustic velocity measured on standing trees (Study **II**, standard errors in parentheses).*

	Correlation with MOE_{SILV}	
	Genetic	Phenotypic
VEL_{TREE}	0.91 (0.05)	0.65 (0.02)
$MOE_{DEN_{CONST}}$	0.91 (0.05)	0.65 (0.02)
$MOE_{DEN_{SILV}}$	0.95 (0.03)	0.75 (0.02)
$MOE_{DEN_{RES.unadjusted}}$	0.87 (0.07)	0.65 (0.02)
$MOE_{DEN_{RES.adjusted}}$ [*]	0.91 (0.05)	0.70 (0.02)
$MOE_{DEN_{PIL}}$	0.84 (0.07)	0.65 (0.02)
$MOE_{DEN_{PIL.B}}$	0.83 (0.08)	0.61 (0.03)

[*] Refers to MOE_{TREE}.

Non-destructive acoustic sensing tools applied at different stages of Scots pine wood processing (standing trees, felled logs and sawn boards) were evaluated in Study **III** (Fundova *et al.*, 2020) using destructively measured sawn-board stiffness (MOE_S) and strength (MOR) as benchmark variables (Table 11). All measures of acoustic-based stiffness (MOE_{TREE}, MOE_{LOG} and MOE_{BOARD}) and acoustic velocity (VEL_{TREE}, VEL_{LOG} and VEL_{BOARD}) provided a good estimate of MOE_S. Moreover, MOE_{TREE}, MOE_{LOG}, VEL_{TREE} and VEL_{LOG} were well correlated with MOR.

Similarly high genetic correlations with the benchmark traits were reported, e.g., for VEL_{LOG} (Cherry *et al.*, 2008; Kumar *et al.*, 2002) and MOE_{LOG} (Fujimoto *et al.*, 2006; Wang *et al.*, 2001). Lower genetic correlations were observed between VEL_{TREE} and MOE_S (Cherry *et al.*, 2008; Kumar *et al.*, 2002).

Table 11. *Additive genetic correlations of destructively measured static moduli of elasticity and modulus of rupture with different dynamic moduli of elasticity and acoustic velocities measured at different stages of wood processing (Study **III**, standard errors in parentheses).*

	$MOE_{S.local}$	$MOE_{S.global}$	MOR
MOE_{TREE}	0.70 (0.22)	0.78 (0.20)	0.90 (0.15)
MOE_{LOG}	0.84 (0.18)	0.85 (0.21)	0.94 (0.13)
MOE_{BOARD}	0.98 (0.07)	0.95 (0.08)	0.62 (0.23)
VEL_{TREE}	0.96 (0.24)	0.97 (0.23)	0.99 (0.23)
VEL_{LOG}	0.92 (0.16)	0.75 (0.21)	0.72 (0.22)
VEL_{BOARD}	0.78 (0.16)	0.65 (0.23)	0.26 (0.33)

4.5 Sawn-board shape stability

Shape stability traits (bow, crook and twist) were considered as the target traits for genetic improvement in Study **IV**. Their direct selection is however infeasible as they cannot be measured until trees are harvested and processed into sawn boards. Improvement of shape stability traits can be accomplished through indirect selection based on selection traits non-destructively measured on standing trees (Table 12).

The strongest additive genetic as well as phenotypic correlation (0.84 and 0.53, respectively) was observed between sawn-board twist (TWI) and standing-tree grain angle (GRA). Similar findings were obtained for Norway spruce (Högberg *et al.*, 2014) and Scots pine (Högberg *et al.*, 2010). A positive genetic correlation (0.62) was also observed between GRA and crook (CRK). The results imply that twisting and crooking of sawn boards could be improved (i.e. decreased) through the selection for lower GRA measured on standing trees.

Table 12. *Additive genetic correlations of sawn-board shape stability traits (bow, crook and twist) with traits non-destructively measured on standing trees (Study **IV**, standard errors in parentheses).*

	BOW	CRK	TWI
DBH	-0.24 (0.30)	-0.54 (0.24)	-0.09 (0.28)
GRA	0.26 (0.29)	0.62 (0.22)	0.84 (0.09)
DEN_{TREE}[*]	-0.07 (0.30)	-0.65 (0.23)	-0.32 (0.25)
VEL_{TREE}	-0.53 (0.37)	-0.49 (0.40)	-0.21 (0.36)
MOE_{TREE}	-0.24 (0.31)	-0.62 (0.26)	-0.30 (0.26)

[*] Refers to $DEN_{RES.adjusted}$.

4.6 Chemical composition of wood

4.6.1 Development of predictive models from FTIR spectra

Models for predicting the chemical composition of juvenile and mature wood from FTIR spectra were developed in Study **V** (Funda *et al.*, 2020). The chemical composition differed between juvenile and mature wood; the former contained 9% less CEL and over 5% more EXT while HEM and LIG were present in the two wood types in similar proportions, with only ca 1% difference. More phenotypic variation (CV_P) was found in mature wood, in particular in EXT (+10.5%) and GAL (+27.2), but the value ranges were greater in juvenile wood (17.8% versus 6.0% and 7.0% versus 5.4% for the two chemical components, respectively).

FTIR spectral profiles of juvenile and mature wood exhibited similar patterns, but distinct differences between them were observed in the region from 1570 to 1750 wavenumbers, where considerably higher variation in absorbance intensities was detected in juvenile than in mature wood, as illustrated in Figure 9. The band position of 1,693 wavenumbers (Figure 9a), at which the greatest variation was observed among juvenile wood samples and which was at the same time missing in most mature wood samples (Figure 9b), was found to be strongly associated with the content of extractives.
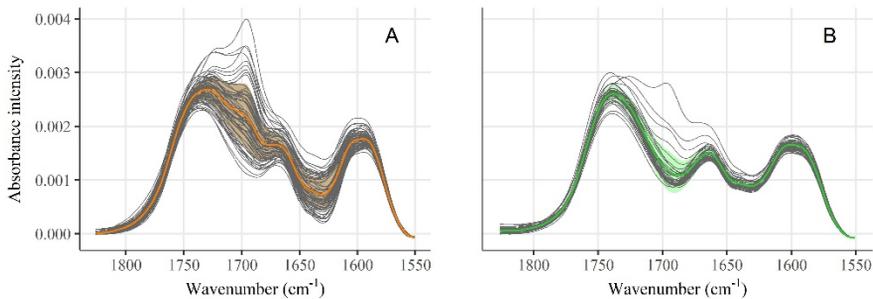
Figure 9. Standardized FTIR spectra of 70 juvenile (A) and 39 mature (B) wood samples of Scots pine in spectral region from 1550 cm^{-1} to 1830 cm^{-1}. The orange and green lines and the highlighted areas around them represent sample means and their standard deviations for given wavenumbers, respectively (Study **V**).

The overall predictive power of the models was good, but highly variable both between juvenile and mature wood and among response variables within the two groups. The best predictive power was attained for EXT in juvenile wood and

for GAL in mature wood ($RMSEP \approx 0.3$), very good for LIG and GAL in juvenile wood and EXT in mature wood ($RMSEP \approx 0.5$), and worst for ARA in juvenile wood and HEM and XYL in mature wood ($RMSEP \approx 0.8$).

The developed models' high predictive powers for EXT and LIG, moderate for CEL and low for HEM (and for some of their structural monosaccharides) are in line with other studies utilizing FTIR spectroscopy for similar purposes (Acquah *et al.*, 2016; Zhou *et al.*, 2015). Results from some other studies using NIR spectroscopy (Acquah *et al.*, 2015; Jones *et al.*, 2006) also showed that predicting HEM with reasonably high accuracies using rapid, non-destructive spectroscopic techniques remains a challenge.

4.6.2 Correlations of chemical compositional traits

Additive genetic correlations among all juvenile wood chemical compositional traits were strong; positive among LIG, CEL and HEM and negative with EXT (Table 13, Study **VI**). Positive relationship between CEL and LIG was however in disagreement with several studies (Lepoittevin *et al.*, 2011; Sykes *et al.*, 2006; Sykes *et al.*, 2003; Pot *et al.*, 2002). One possible reason could be the variation in EXT, which was herein substantially greater (range 0.8%–29.6%, $CV_P = 54.9\%$ and $CV_A = 34.5\%$) compared to other studies, e.g., Lepoittevin *et al.* (2011) (range 3.3%–10.3%, $CV_P = 19.0\%$, $CV_A = 11.3\%$). Since the chemical compositional traits are expressed as relative proportions summing up to 1 (or 100%), the presence of one trait (or a group of traits) can only occur at the expense of another trait.

All genetic correlations between chemical compositional traits and wood quality traits were weakly to moderately negative, except for those with EXT, which were moderately positive. Moderate negative relationship between LIG and wood density is in congruence with Pot *et al.* (2002) and Porth *et al.* (2013).

Table 13. *Additive genetic correlations among chemical compositional traits and their correlations with traits non-destructively measured on standing trees on site Vännäsby (Study **VI**, standard errors in parentheses).*

	LIG	CEL	HEM	EXT
DBH	0.42 (0.27)	0.30 (0.32)	0.13 (0.25)	-0.19 (0.26)
DEN_{TREE}[*]	-0.42 (0.19)	-0.37 (0.23)	-0.49 (0.17)	0.45 (0.18)
MOE_{TREE}	-0.61 (0.17)	-0.35 (0.25)	-0.63 (0.15)	0.51 (0.18)
LIG	1	0.80 (0.15)	0.87 (0.07)	-0.95 (0.05)
CEL	0.80 (0.15)	1	0.78 (0.13)	-0.88 (0.08)
HEM	0.87 (0.07)	0.78 (0.13)	1	-1.00 (0.02)

[*]Refers to $DEN_{RES.adjusted}$.

4.7 Genetic correlations between growth and wood quality traits

Low to moderate negative additive genetic correlations estimated between growth and wood quality traits in the studies underlying this thesis (Tables 14 and 15) were in line with earlier studies on Scots pine (Hong *et al.*, 2014; Fries, 2012; Fries & Ericsson, 2006; Hannrup *et al.*, 2000) and other conifer species (El-Kassaby *et al.*, 2011; Eckard *et al.*, 2010; Li & Wu, 2005; Kumar *et al.*, 2002; Pot *et al.*, 2002; Zhang & Morgenstern, 1995). Negative genetic correlations imply that selection for growth results in lower wood quality and vice versa. In addition, prioritizing growth traits increases microfibril angle (MFA), which negatively influences the quality of end-products such as sawn-board stiffness (Ivković *et al.*, 2007) or pulp yield (Apiolaza *et al.*, 2005).

Table 14. *Additive genetic correlations of diameter at breast height with wood quality traits measured on sawn boards (Study **III**, standard errors in parentheses).*

	DEN_{VOL}	MOE_{BOARD}	$MOE_{S.local}$	$MOE_{S.global}$	MOR
DBH	-0.39 (0.23)	-0.49 (0.23)	-0.34 (0.30)	-0.47 (0.28)	-0.03 (0.32)

Table 15. *Additive genetic correlations of growth traits with wood quality traits non-destructively measured on standing trees (Studies **I** & **II**, standard errors in parentheses).*

	DEN_{SILV}	$DEN_{RES.adjusted}$	$DEN_{PIL.B}$	MOE_{SILV}	VEL_{TREE}	$MOE_{DEN_{RES.adjusted}}$
DBH	-0.47 (0.18)	-0.45 (0.19)	-0.50 (0.19)	-0.45 (0.18)	-0.26 (0.21)	-0.32 (0.21)
HGT	-0.27 (0.19)	-0.20 (0.21)	-0.22 (0.22)	-0.38 (0.19)	-0.18 (0.21)	-0.26 (0.20)
VOL	-0.44 (0.19)	-0.41 (0.20)	-0.49 (0.20)	-0.44 (0.19)	-0.24 (0.21)	-0.30 (0.21)

4.8 Index selection

Index selection was applied in Study **II** (Fundova *et al.*, 2019) to investigate the possibility of simultaneous improvement of growth and wood quality traits, despite the negative genetic correlation between them (Cotterill & Dean, 1990; Hazel, 1943). Different sets of non-monetary weights for MOE and DEN relative to 1 for DBH were plotted against expected genetic gains (Figure 10), through which regions with positive gains for both traits were revealed. Intersections of the two respective curves were considered as points of good compromises, and weights corresponding to these intersections were used for calculating index coefficients. Weights determined for simultaneous selection of DBH and

MOE$_{SILV}$ (1 cm for DHB and 1 GPa for MOE) corresponded with those estimated by Chen *et al.* (2016b) and Hayatgheibi *et al.* (2019).
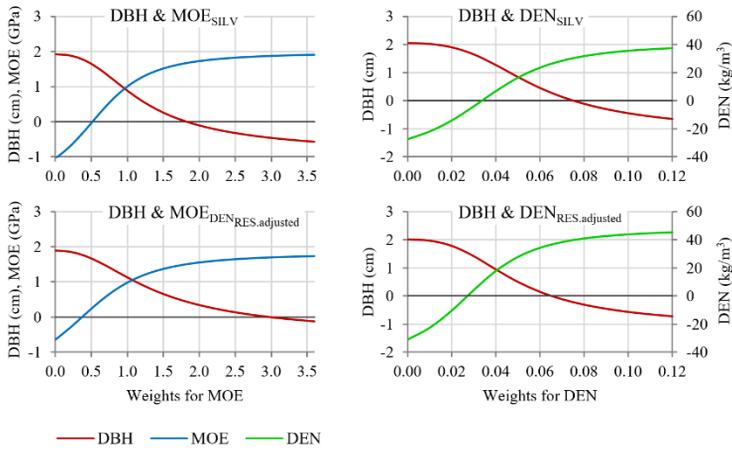

Figure 10. Expected genetic gains for simultaneous selection of stem diameter (DBH) with different moduli of elasticity (MOE) and wood density (DEN). X-axis shows weights for MOE and DEN relative to a constant of 1 for DHB; Y-axis shows expected genetic gain with 1% selection intensity. MOE$_{DEN_{RES.adjusted}}$ refers to MOE$_{TREE}$ (Study **II**).

4.9 Genetic gain and response to selection

Selection exclusively for DBH resulted in a positive response of other growth traits but negative response of wood quality traits and unfavourable positive response of MFA (Table 16). Selection for either MOE$_{SILV}$ or DEN$_{RES.adjusted}$ had an opposite effect. All indices constructed for simultaneous improvement of growth and wood quality led to desirable improvement of all target traits including MFA. The combination of DBH and MOE$_{DEN_{RES.adjusted}}$ calculated from standing tree acoustic velocity and adjusted resistograph density appears to be the most efficient strategy.

Single-trait selection aiming at higher DBH, DEN$_{TREE}$, VEL$_{TREE}$ and MOE$_{TREE}$ as well as lower GRA resulted in lower BOW, CRK and TWI in Study **IV** (Table 17). GRA, non-destructively measured on standing-trees, seems to be the optimum choice for genetic improvement of sawn-board shape stability. Selection for lower GRA also appears to have a positive effect on sawn-board density, stiffness and strength (Table 6 in Study **IV**).

Table 16. *Genetic gain (in parentheses) and correlated genetic response (both in %) for important growth and wood quality traits (individually and combined) under 1% selection intensity (Studies I and II). Weights (in square brackets) correspond to intersections of plotted weights versus expected genetic gains (Figure 10) and were used for calculating index coefficients.*

Selection trait	Weight	Response in target trait				
		DBH (9.40)	VOL (20.04)	MOE_{SILV} (19.27)	DEN_{SILV} (9.07)	MFA (19.18)
DBH	-	9.40	19.75	-6.47	-2.90	5.66
MOE_{SILV}	-	-5.69	-11.85	19.27	7.02	-19.62
$DEN_{RES.adjusted}$	-	-6.01	-11.51	12.27	8.45	-4.71
DBH & MOE_{SILV}	[1 1.0]	4.04	8.61	9.57	2.95	-10.75
DBH & $MOE_{DEN_{RES.adjusted}}$ [*]	[1 1.1]	4.95	10.03	9.83	4.31	-8.60
DBH & DEN_{SILV}	[1 0.05]	5.39	11.63	3.65	2.24	-1.94
DBH & $DEN_{RES.adjusted}$	[1 0.04]	3.16	6.87	5.93	4.50	-0.86

[*] Refers to MOE_{TREE}.

Table 17. *Correlated genetic response of shape stability traits to selection based on stem diameter and several wood quality traits non-destructively measured on standing trees under 1% selection intensity (Study IV). The arrows indicate the direction of intended selection.*

Selection traits		Response in selection traits	Response in target traits		
			BOW [mm]	CRK [mm]	TWI [mm]
DBH	↑	15.19%	-0.50	-0.57	-0.23
DEN_{TREE} [*]	↑	10.97%	-0.19	-0.89	-1.07
VEL_{TREE}	↑	0.89%	-0.51	-0.24	-0.25
MOE_{TREE}	↑	11.28%	-0.48	-0.63	-0.74
GRA	↓	2.02°	-0.70	-0.85	-2.80

[*] Refers to $DEN_{RES.adjusted}$.

5   Conclusions and Future perspectives

This thesis presents the evaluation of different assessment methods for various wood quality traits important for construction, pulp & paper and bioenergy industries. The emphasis was put on reliability, non-destructiveness, applicability *in-situ* on standing trees, rapidity and cost efficiency. Based on the six studies underlying this thesis, the following conclusions can be drawn:

1. Resistograph, a tool that is based on drilling resistance, proved to be suitable for non-destructive wood density assessment of Scots pine standing trees, in particular when drilling profiles are adjusted for accumulated needle friction.

2. Pilodyn, a tool that measures penetration depth of a pin, does not seem to be as suitable as the resistograph for wood density assessment of Scots pine, even if a patch of bark is removed prior to the measurement.

3. Acoustic velocity combined with adjusted resistograph density performed best in the test of different approaches of calculating standing-tree dynamic modulus of elasticity. It was closely followed by acoustic velocity combined with constant density and the acoustic velocity alone.

4. Non-destructive acoustic sensing tools applied on standing trees, felled logs and sawn boards proved to be capable of accurately predicting the destructively measured sawn board stiffness (either as acoustic velocities or dynamic moduli of elasticity calculated from them).

5. Standing-tree acoustic velocity, adjusted resistograph density and modulus of elasticity calculated from them well reflect sawn board strength.

6. Selective breeding for lower grain angle would improve sawn board quality, i.e. lower twist, crook, and bow and higher density, stiffness and strength.

7. Fourier transform infrared (FTIR) spectroscopy proved to be suitable for rapid and non-destructive assessment of the chemical composition of juvenile and mature wood in Scots pine.

8. Despite the negative genetic correlations observed between growth and wood quality traits, it would be possible to perform simultaneous genetic improvement for these traits. An index combining diameter at breast height and modulus of elasticity calculated from adjusted resistograph density and acoustic velocity measured on standing trees provided the best compromise for simultaneous improvement of growth, fibre and wood quality traits.

Future perspectives of Scots pine genetic improvement may include:

1. Implementation of wood quality measurements (resistograph density and/or standing-tree acoustic velocity) into the routine procedures so that breeding values predicted from numerous progeny trials could be used for breeding selection purposes.

2. Development of economic breeding objectives (economic weights) for maximizing profits from tree breeding for sawn timber, pulp & paper and biofuel producing industries.

3. Application of genomic selection to reduce the length of the breeding cycle and accelerate the genetic gain.

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Popular science summary

Wood is a natural, renewable and versatile material that has been utilized by humans for millennia for a great variety of industrial and domestic purposes. Its usefulness for different products depends on properties that are collectively called "wood quality". For instance, construction boards must be stiff and strong and must not twist or crook, while paper and bioethanol production requires high proportion of cellulose

In forest tree breeding, superior trees are selected and crossed with the aim of producing the next generation of forests with "better" properties. Until the recent past, emphasis was mostly put on increasing stem volume. However, growth and wood quality traits in conifer tree species are usually negatively correlated, meaning that one can only be improved at the expense of another. In other words, prioritizing growth would in a longer term lead to the deterioration of wood quality. It is therefore important to incorporate wood quality into forest tree improvement programs.

Growth traits such as height or stem diameter are relatively easy to measure on standing trees but measuring wood quality might be tricky. It must not hurt the trees so that they can be preserved for further breeding. I have tested the suitability of various methods for rapid and non-destructive assessment of wood quality traits, important for construction, pulp & paper and bioenergy industries, on Scots pine standing trees and evaluated their potential for genetic improvement.

Populärvetenskaplig sammanfattning

Trä är ett naturligt, förnybart och mångsidigt material som har använts av människor i årtusenden för såväl industri- som hushållsändamål. Användbarheten för olika produkter beror på virkets egenskaper. Till exempel måste konstruktionsvirke vara styvt och starkt och får inte vrida sig eller vara krokigt, medan papper och bioetanolproduktion kräver en stor andel cellulosa.

Vid förädling av skogsträd väljs och korsas träd av god kvalitet med målet att producera nästa generation skogar med "förbättrade" virkesegenskaper. Förädlingen har hittills i huvudsak varit inriktad på att öka stamvolymen. Men tillväxt och vedkvalitet hos barrträd är vanligtvis negativt korrelerade, vilket innebär att tillväxt förbättras på bekostnad av vedkvalitet. Med andra ord skulle en prioritering av enbart tillväxt på längre sikt kunna leda till försämrad vedkvalitet. Det är därför viktigt att integrera vedkvalitet i förädlingsprogram för skogsträd.

Tillväxtegenskaper som höjd och stamdiameter är relativt enkla att mäta på stående träd, men att mäta vedkvalitet kan vara svårt. Mätningen får inte skada träden så att de inte kan bevaras för vidare förädling. Olika metoder för snabb och icke-förstörande bedömning av vedegenskaper som är viktiga för byggbranschen, massa & papper och bioenergi har testats. Mätningarna har gjorts på stående tallar och potentialen för genetisk förbättring har utvärderats.

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