Genetic analysis of fiber-dimension traits and combined selection for simultaneous improvement of growth and stiffness in lodgepole pine (Pinus contorta)

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<th>Journal:</th>
<th>Canadian Journal of Forest Research</th>
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<tr>
<td>Manuscript ID</td>
<td>cjfr-2018-0445.R2</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>11-Jan-2019</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Hayatgheibi, Haleh; Umea Plant Science Centre Fries, Anders; Swedish University of Agricultural Sciences, Department of Forest Genetics and Plant Physiology Kroon, Johan; Skogforsk Wu, Harry; Swedish University of Agriculture Sciences, Forest Genetics and Plant Physiology; CSIRO, Plant Industry</td>
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<tr>
<td>Keyword:</td>
<td>Pinus contorta, fibre-dimension properties, selection index, genetic gain, early selection</td>
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<td>Is the invited manuscript for consideration in a Special Issue?:</td>
<td>Not applicable (regular submission)</td>
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Genetic analysis of fiber-dimension traits and combined selection for simultaneous improvement of growth and stiffness in lodgepole pine (*Pinus contorta*)

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Abstract

Quantitative genetic variation of fiber-dimension traits and their relationship with diameter at breast height (DBH) and solid-wood traits (i.e. density and modulus of elasticity (MOE)) was investigated in lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.). A total of 823 increment cores were sampled from 207 half-sib families at two independent progeny trials, aged 34-35 year, located in northern Sweden. High-resolution pith-to-bark profiles were obtained for radial fiber width (RFW), tangential fiber width (TFW), fiber wall thickness (FWT), and fiber coarseness (FC) using SilviScan. Heritabilities ranged from 0.29 to 0.74 and inheritance increased with cambial maturity. Estimated age-age genetic correlations indicate that early selection between ages 5 and 8 years is highly efficient. Our results indicate that selection for a 1% increase in DBH or MOE incurs a negligible effect on fiber-dimension traits and maximum genetic gains are reached when DBH and MOE are considered jointly. Moreover, simultaneous improvement of growth and stiffness is achievable when a selection index with 7 to 10 economical weights for MOE relative to 1 for DBH is incorporated. However, the unfavorable relationship between solid-wood and pulp and paper-related traits suggests that breeding strategies must be implemented to improve wood quality of lodgepole pine for multiple uses.

Key words: *Pinus contorta*, fiber-dimension properties, selection index, genetic gain, early selection
59 **Introduction**
60 Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.) are the two most important
61 native tree species for commercial wood production in Sweden. However, during the 1970s, the North
62 American lodgepole pine (*Pinus contorta* Doug. ex Loud. var. *latifolia* Engelm.) was adopted as the
63 third main conifer species to mitigate the predicted future shortage of timber in Sweden (Hagner
64 1983). The introduction of lodgepole pine, primarily for pulpwood production (Backlund and Bergsten
65 2012), was accompanied by extensive transfer of seed and breeding materials collected from natural
66 stands distributed in western Canada (Bartram 1980; Ericsson 1993). Today, more than 600,000 ha of
67 Swedish forest area is covered by lodgepole pine (Elfvíng et al. 2001) and its superiority over Scots
68 pine in terms of growth, survival, damage resistance and productivity (Elfvíng and Norgren 1993;
69 Ericsson 1993) enhances its potential as a plantation species for pulpwood and solid-timber
70 production.

Wood properties play a significant role in the health of plantations and quality of final products; however, they have been neglected in selection of lodgepole pine breeding populations in the past. Stem bending, breakage, and general instability of lodgepole pine due to wind and snow load has been a major issue in northern Sweden. A previous study by Fries et al. (2014) which investigated stem damage of lodgepole pine clonal cuttings in relation to wood properties, revealed that the clones with lower density, lower stiffness, and higher microfibril angle (MFA) tend to have a higher proportion of stem damage (Fries et al. 2014).

Wood density is regarded to be the major trait, influencing yield and quality of fiber products, quality of solid-wood products, and energy consumption of pulping (Zobel and van Buijtenen 1989). Wood density is a combination of wood properties including cell diameter, cell wall thickness, and proportion of latewood (Zobel and Jett 1995). These wood properties exhibit continuous variation and thus are considered as quantitative traits controlled by multiple genetic and environmental factors (Thamarus et al. 2004). Genetics of wood quality traits have been extensively studied in recent years (Wu et al. 2008). Strong genetic control for most wood quality traits such as density and stiffness has already been confirmed in various conifers (Gräns et al. 2009; Li et al. 2007; Wu et al. 2008).
Estimated genetic correlations between growth and density or modulus of elasticity (MOE) were mostly negative, primarily in radiata pine (Pinus radiata D. Don) (Baltunis et al. 2007), Scots pine (Fries 2012; Hong et al. 2014), Norway spruce (Chen et al. 2014; Hannrup et al. 2004), and lodgepole pine (Hayatgheibi et al. 2017).

One of the fundamental goals in tree breeding programs is to make genetic gains as early as possible by reducing the time of breeding cycle with early selection. High age-age genetic correlations between the early and the late reference age and high heritability estimates at early age could make early selections highly efficient (Lenz et al. 2011). In general, early selection is more efficient for wood quality traits than growth traits (Li and Wu 2005, Wu et al. 2007).

Variation of wood fiber-properties is of particular importance for the pulp and paper industry, since the structure of the wood fibers used as raw material is a good predictor of the quality of pulp and paper final-products. In addition to density, MFA (the angle between cellulose microfibrils of the cell wall and the longitudinal axis of the cell (Cave and Walker 1994)), fiber length, fiber coarseness (FC) and fiber wall thickness (FWT) also affect pulp and paper properties (Ramirez et al. 2009; Scallan and Green 1974). FC affects sheet formation, tensile strength and absorption capacity (Zhu et al. 2008). Low MFA as well as long and slender fibers enhance tensile strength in paper (Donaldson 1993) and fine fibers collapse more easily and cause better bonding during sheet formation (King et al. 1998). Coarseness, defined as fiber mass per fiber length (Carrillo et al. 2015), is influenced by cell wall thickness, fiber width and cell wall density (Mansfield et al. 2007). Thin-walled fibers 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. 2010).

Despite their importance, genetic studies on anatomical wood traits are limited owing to the difficulty in measuring such traits. Nevertheless, genetic control, age trends of inheritance, and relationships of fiber-dimension traits with growth and solid-wood traits have been described for several conifers, including Scots pine (Fries 2012; Hannrup and Ekberg 1998; Hannrup et al. 2000; Hong et al. 2014, 2015), Norway Spruce (Chen et al. 2016), and white spruce (Picea glauca MoenchVoss.) (Lenz et al. 2011). Results of these studies have confirmed a moderate to high genetic control as well as high age-age genetic correlations for fiber-dimension traits, indicating possible
genetic gains are expected in advanced improvement programs of such traits. Furthermore, observed adverse influence on stem wood density or stiffness (Bendtsen 1978; Rozenberg and Cahalan 1997). In general, unfavorable genetic correlations remain as a constraint in tree improvement programs. However, there are several ways described in the literature to overcome such difficulties, including designing effective breeding strategies (Hallingbäck et al. 2014; Wu and Sanchez 2011; Yanchuk and Sanchez 2011), applying restricted index selection (Chen et al. 2016; Gapare et al. 2009), and using index selection with optimal economic weights for improving several traits simultaneously (Ivkovic´ et al. 2010; Ivkovic´ et al. 2006).

The original purpose of establishing lodgepole pine plantations in Sweden was to serve the pulp and paper industries, and to date, breeding efforts have been focusing mainly on its climate adaptability, survival, growth and stem quality. Understanding the genetic variation of pulp and paper-related properties, identification of the factors causing such variation and investigation of their relationship with growth and other wood properties is therefore a major prerequisite for further selection and development of the species (Apiolaza 2009; Raymond 2002).

Age trends of inheritance, age-age genetic correlations and the efficiency of early age selection for growth and solid-wood properties of lodgepole pine have been investigated in a previous study (Hayatgheibi et al. 2017). Growth showed a negative genetic correlation with wood stiffness, and thus index selection with appropriate economical weights were recommended in order to find superior individuals in terms of both growth and stiffness in advanced breeding programs of the species.

Genetic control of fiber-dimension traits and their relationship with growth and solid-wood traits have not yet been investigated in Swedish lodgepole pine populations. Therefore, the overall focus of this study was to explore the genetic control of fiber-dimension traits, e.g. radial fiber width
(RFW), tangential fiber width (TFW), FWT and FC using two Swedish lodgepole pine progeny trials of the previous study (Hayatgheibi et al. 2017). The specific objectives were to: 1) estimate genetic variation and heritability for fiber-dimension traits, 2) evaluate genetic and phenotypic correlation of fiber-dimension traits with growth and solid-wood traits, 3) estimate age-age genetic correlation and efficiency of early age selection, and 4) evaluate possible genetic gain using different selection scenarios.

Materials and methods

Study materials and measurements

Two lodgepole pine progeny trials located in northern Sweden, Övra (Skogforsk S23F8060373; latitude 63°57' N, longitude 16°46' E) and Lagfors (Skogforsk S23F7960; latitude 62°45' N, longitude 17°08' E), were sampled for this study. Övra with 178 open-pollinated families originating from four geographic regions (provenances) (Fort Nelson, Watson Lake, Fort St. John and Prince George) was planted in 1980. Lagfors with 214 open-pollinated families originating from two provenances (Fort St. John and Prince George) was planted in 1979. These families at both trials were planted in a randomized complete block design with five replicates (block). Each family was planted in 10-tree and 12-row plots in each block, resulting in 50 planted trees per family. There were no common families between the two trials. More details on trials characteristics and sampling design have been further described in Hayatgheibi et al. (2017).

At the age 34 and 35, respectively, single 12-mm bark-to-bark increment-cores were collected at breast height (1.3 m) from 399 trees at Övra (about four trees from 100 families), and from 423 trees (about four trees from 107 families) at Lagfors and assessed by SilviScan instrument (Innventia AB, Stockholm, Sweden). High-resolution pith-to-bark radial variations were obtained for solid-wood (Hayatgheibi et al. 2017) and fiber-dimension traits including radial fiber width (RFW), tangential fiber width (TFW), fiber wall thickness (FWT) and fiber coarseness (FC) measured as averages for consecutive 25 µm radial intervals (Evans 1994; Evans 2006; Evans et al. 1995).

The variation of wood properties from the SilviScan measurement was analysed for each annual ring and at the whole core level. The area-weighted value (AWV), representing the average properties of the wood more accurately, was calculated for each trait as follows:
1) \( AWV = \frac{\sum (a_id_i)}{\sum a_i} \)

where \( a_i \) is the cross-sectional area of annual ring \( i \), assuming that each ring is circular, and \( d_i \) is the value of annual ring \( i \) (Hannrup et al. 2000). In addition, a complete assessment of diameter at breast height (DBH), vitality, damages and general condition (i.e. double stem) was made at the age 34 years on 4329 trees at Övra, and at the age 36 years on 6289 trees at Lagfors.

**Statistical analysis**

Variance and covariance components for genetic analysis were estimated using ASReml statistical software package (Gilmour et al. 2009) based on the following linear mixed-effects model for single-site analysis:

\[
y_{jklm} = \mu + P_k + B_j + F_{l(k)} + BF_{jl(k)} + e_{jklm}
\]

where \( y \) is the vector of observations on tree \( m \) from family \( l \) within provenance \( k \) in block \( j \), \( \mu \) is the overall mean, and \( P_k \) and \( B_j \) are the fixed effects of the provenance \( k \) and the block \( j \), respectively. The variable \( F_{l(k)} \) is the random effect of the family \( l \) within the provenance \( k \), \( BF_{jl(k)} \) is the random interactive effect of the block \( j \) and the family \( l \) within the provenance \( k \), and \( e_{jklm} \) is the random residual effect.

Estimates of heritability were obtained for each trait at each trial using the variance components from the univariate single-site analysis. Standard errors were estimated using the Taylor series expansion method (Gilmour et al. 2009). The individual-tree narrow-sense heritability (\( h^2 \)) for each trait at each trial was calculated using the following equation assuming these open-polinated families are half-sib families (Falconer and Mackay 1996).

\[
ah^2_i = \frac{\sigma^2_A}{\sigma^2_p} = \frac{4 \times \sigma^2_f}{\sigma^2_y + \sigma^2_{bf} + \sigma^2_e}
\]

where \( \sigma^2_A \) is the additive genetic variance, \( \sigma^2_p \) is the phenotypic variance, \( \sigma^2_f \) is among-family variance, \( \sigma^2_{bf} \) is the family by block variance, and \( \sigma^2_e \) is the residual variance. Genetic and phenotypic correlations (type A) between traits \( x \) and \( y \) (\( r_{(xy)} \)), and age-age genetic correlations were calculated using the following model:

\[
r_{(xy)} = \frac{\text{Cov}(x,y)}{\sqrt{\sigma^2_x \times \sigma^2_y}}
\]
where $\hat{\text{Cov}}_{(x,y)}$ is the estimated phenotypic or genetic covariance between traits $x$ and $y$ or between early age and reference age (ring 26), $\hat{\sigma}^2_{(x)}$ is the estimated additive genetic variance for trait $x$ or for early age, and $\hat{\sigma}^2_{(y)}$ is the estimated additive genetic variance for trait $y$ or for the reference age.

The efficiency of early age selection ($E_{gen}$) relative to reference age for each trait is calculated as

$$E_{gen} = \frac{i_E h_E}{r_A i_A h_A}$$

where $r_A$ is the additive genetic correlation between the early and the reference ages, $i_E$ and $i_A$ are the selection intensities at the early and at the reference age, respectively, and $h_E$ and $h_A$ are the square roots of $h^2$ at the early age and the reference age, respectively (White et al. 2007). Selection intensities at early age and the reference age were assumed equal.

**Index selection and responses to different selection scenarios**

Economic weights for growth and stiffness (DBH and MOE, respectively) in lodgepole pine have not been estimated using production-system parameter estimates. A 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, when the economic weights of growth and MOE used in radiata pine (Ivkovic´ et al. 2006) were applied. To examine the importance of relative weights of DBH and MOE in lodgepole pine, the selection index with different sets of economic weights for MOE, ranging from 5 to 15 relative to 1 for DBH, was applied. Multiple iterations using the Smith-Hazel index (Hazel 1943; Smith 1936) were performed to find sets of optimum economic weights with desired genetic gains for both traits. The index ($I$) is written as:

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

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

$$b = P^{-1} G a$$

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 (from 5 to 15 for MOE, 1 for DBH).
The expected genetic gain (Δ4) of each individual trait included in a Smith-Hazel index was calculated as (Cotterill and Dean 1990; Turner and Young 1969):

\[
\Delta A_x = i \left( \frac{b_x V_{Ax} + b_y COV_{Ax,y}}{\sigma_i} \right)
\]

where \(\Delta A_x\) 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 \(x\), \(COV_{Ax,y}\) 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 \(\sigma_i\) is the phenotypic standard deviation of the index.

The optimal selection strategy for DBH and MOE was defined in terms of their respective positive genetic responses to selection based on optimum sets of economic weightings of MOE relative to DBH. Additionally, to evaluate genetic responses of density and fiber-dimension traits to selection based on growth and stiffness, three different selection scenarios were considered:

A) Selection based on DBH alone, B) selection based on MOE alone, and C) index selection based on combining MOE and DBH with economic weightings of 10 for MOE relative to 1 for DBH.

The correlated response of the target trait \(t\) (\(CR_t\)) based on indirect selection of correlated trait \(j\) was calculated as:

\[
CR_t = i \times h_j \times h_t \times r_A \times CV_t
\]

where \(i\) is the selection intensity of 1% (\(i=2.667\)), \(h_j\) and \(h_t\) are the square root of narrow-sense heritability for the selected trait and the target trait, respectively, \(r_A\) is the additive genetic correlation between the traits, and \(CV_t\) is the phenotypic coefficient of variation for the target trait \(t\).

Results

Phenotypic trends

Area-weighted wood density, modulus of elasticity (MOE), fiber wall thickness (FWT), and fiber coarseness (FC) were higher in Lagfors, while diameter at breast height (DBH), area-weighted radial fiber width (RFW), tangential fiber width (TFW), and microfibril angle (MFA) were higher in Övra (Table 1). Age trends of fiber-dimension traits were approximately similar at both trials (Fig. 1). RFW increased from 25 µm at ring 2 to about maximum value of 33 µm at ring 15 before falling to around 32 µm in Övra and around 30 µm in Lagfors at the bark. TFW at both trials was about 26 µm near the
pith and increased steadily until it reached to about 30 µm at the bark. Mean FWT increased from about 2 µm close to the pith, reached around 2.6 µm at ring 18 in Övra and around 3 µm at ring 19 in Lagfors, and stabilized towards the bark. FC showed a similar trend as FWT, as the mean FC was minimum near the pith at both trials (about 300 µg/m) and reached the maximum at ring 20 (about 440 and 470 µg/m in Övra and Lagfors, respectively) and stabilized towards the bark.

**Trend for heritability**

Individual-tree narrow-sense heritability estimates ($h^2$) for cumulative area-weighted RFW, TFW, FWT and FC from annual ring 1 to annual ring 26 are presented in Fig. 2. In general, all estimated heritabilities were greater in Lagfors than in Övra and heritabilities increased with cambial maturity at both trials. Heritability for RFW at both trials increased from 0.2 near the pith to a maximum of about 1 in Lagfors and 0.6 in Övra in rings 10 to 12. After that, the heritability in Lagfors declined to about 0.7 towards the bark, while it remained the same in Övra. Heritability for TFW in both trials was about zero near the pith, then increased to a peak of about 0.8 in Lagfors and 0.4 in Övra at ring 12, and then stabilized towards the bark. In Lagfors, heritability trends for FWT and FC were similar, as heritabilities of both traits increased from the pith to a maximum of about 0.8 at ring 13 and then stabilized towards the bark. Similarly, such heritabilities at Övra reached a maximum at ring 13 (about 0.4). After that, heritability of FWT declined to about 0.2 towards the bark, while it remained the same (about 0.4) for FC.

**Age-age genetic correlations**

Age-age genetic correlations between each of the rings and the reference ring at age 26 years for cumulative area-weighted RFW, TFW, FWT and FC are presented in Fig. 3. The age-age genetic correlations were very high and reached unity from ring 6 onwards for all studied traits at both trials. The age-age genetic correlation at earlier ages was higher in Lagfors than in Övra for all traits except for FWT.

**Early selection efficiency**
Efficiency of early selection relative to selection based on the reference ring 26 calculated for cumulative area-weighted RFW, TFW, FWT and FC was very high at both trials and efficiency increased rapidly along the selection rings (Fig. 4). Early selection efficiencies were slightly greater in Lagfors than in Övra, except for FWT, which reached unity from the first rings in Övra, while such efficiency was achieved at ring 8 in Lagfors. Early selection efficiencies for RFW and FC in Lagfors reached about 1 at rings 5 and 7, respectively, while such efficiencies in Övra were achieved at rings 10 and 13, respectively. Early selections for TFW at rings 8 and 11 for Lagfors and Övra, respectively, were as efficient as the reference ring.

Correlations of DBH and solid-wood traits with fiber-dimension traits

Estimated phenotypic and genetic correlations among DBH, solid-wood properties and fiber-dimension traits are presented in Table 2. Overall, the estimated genetic and phenotypic correlations between pairs of traits were consistent across both trials with the exception of some correlations of MFA and MOE with other traits. At both trials, DBH had moderate positive genetic correlations with RFW, TFW and FC (ranging from 0.28 to 0.67), whereas it showed non-significant correlations with FWT (0.1 at Övra and -0.03 at Lagfors). MFA had non-significant correlations with FWT and FC in Övra, while those correlations were moderate positive in Lagfors (0.40 and 0.30, respectively). At both trials, genetic correlations of MFA with RFW were around zero, while its correlations with TFW were negative (-0.19 in Övra and -0.56 in Lagfors).

At Övra, MOE showed negative genetic correlations with RFW (-0.33) and TFW (-0.30), while those correlations were around zero and positive (-0.08 and 0.58, respectively) in Lagfors. At both trials, MOE had positive genetic correlations with FWT (0.66 in Övra and 0.26 in Lagfors) and FC (0.28 in Övra and 0.39 in Lagfors). Density showed negative genetic correlations with RFW (-0.48 in Övra and -0.31 in Lagfors) and TFW (-0.71 in Övra and -0.20 in Lagfors), whereas its correlations were positive with FWT (0.90 in Övra and 0.91 in Lagfors) and FC (0.39 in Övra and 0.60 in Lagfors).

Correlations among fiber traits

At both trials, genetic correlations of FC with FWT (0.78 in Övra, 0.87 in Lagfors), RFW (0.55 in Övra, 0.45 in Lagfors) and TFW (0.20 in Övra, 0.39 in Lagfors) were positive. Similarly, positive
genetic correlations were observed between RFW and TFW (0.53 in Övra and 0.20 in Lagfors). In contrast, FWT showed negative correlations with RFW (-0.14) and TFW (-0.53) in Övra, while its genetic correlations were around zero (0.03 and 0.09, respectively) in Lagfors.

Response for different selection scenarios

Expected genetic responses for DBH and MOE based on selection index (DBH and MOE) with indicated economic weights ranging from 5 to 15 for MOE relative to 1 for DBH are shown in Fig. 5. As the economic weighting of MOE decreased from the default 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. The economic weighting of MOE ranging from 7 to 10 resulted in positive genetic gains for both traits.

Joint-site correlated genetic gains ($CR_t$) based on three selection scenarios with a 1% selection intensity ($i = 2.67$) are presented in Table 3. Scenario A: selection for increase in DBH alone resulted in a slight decrease of density (-1.5%) and a slight increase of RFW (2.1%), TFW (1.0 %), FWT (0.2%), and FC (2.5%). Scenario B: selection for increase of MOE alone incurred a negligible decrease in RFW (-1.6%) and a slight increase in density (3.2%) and other fiber traits. Scenario C: selection index combining DBH and MOE using economic weights (10 for MOE relative to 1 for DBH) led to a negligible increase in RFW (0.2%) and a slight increase in TFW (1.5%), FWT (3.6%), FC (4.4%), and density (2.3%).

Discussion

Mean values and phenotypic trends

The phenotypic trends observed for fiber traits in this study (Fig. 1) agree well with previous reports in other conifers such as Norway spruce (Chen et al. 2016), Scots pine (Hong et al. 2015) and white spruce (Lenz et al. 2010), as the mean values of all four fiber traits (radial fiber width (RFW), tangential fiber width (TFW), fiber wall thickness (FWT), and fiber coarseness (FC)) were lower near the pith and increased steadily with the cambial maturity. Although the two progeny trials investigated in this study were genetically unrelated, the phenotypic trends observed for their fiber traits were generally similar. However, after age 18 years, FWT and FC were greater in Lagfors than in Övra,
while RFW was less. This finding is consistent with results of the recent report in lodgepole pine, as density and latewood proportion after age 18 years were greater in Lagfors than in Övra, while growth (ring width) was less (Hayatgheibi et al. 2017).

Experimental results investigating the influence of fertilization on fiber-dimension properties documented that trees growing at fertile sites (faster growth) have greater radial cell width and reduced cell wall thickness (Lundgren 2004; Nyakuengama et al. 2003). In this study, we observed that trees growing at Övra have higher RFW, while they have lower FC and lower FWT (Table 1), which may be attributed to the slightly faster growth at Övra.

**Genetic parameters**

In general, fiber-dimension traits are reported to be highly heritable (Zobel and Jett 1995). High heritability estimates obtained for area-weighted RFW, TFW, FWT and FC in this study (0.29- 0.71 in Övra and 0.72 to 0.74 in Lagfors) were even greater than those reported in Scots pine (Hannrup et al. 2000; Hong et al. 2014), Norway spruce (Chen et al. 2016) and white spruce (Ivkovich et al. 2002; Lenz et al. 2010). The inheritance pattern from pith to bark was also investigated for each trait (Fig 2). The lowest heritability estimates were observed in rings near the pith and heritability peaked around the annual ring 12 and then stabilized towards the bark in both trials. Although the pattern for heritability was very similar at both trials, individual-ring as well as whole-core heritability estimates were greater in Lagfors than in Övra, as was the case with heritability estimates of density (Hayatgheibi et al. 2017). Increasing heritability for RFW, TFW, FWT and FC from pith to bark had also been observed in white spruce (Lenz et al. 2010; Lenz et al. 2011), Norway spruce (Chen et al. 2016) and Scots pine (Hong et al. 2015).

In order to implement a successful breeding program for wood properties, it is essential to determine how different wood properties relate to one another, as selection for one desired property might reduce the value of another property (Zobel and Jett 1995). For instance, it has been noted that density has a negative and unfavourable correlation with RFW (Chen et al. 2016; Hannrup et al. 2000; Ivkovich et al. 2002; Lenz et al. 2010), while it has a positive correlation with FWT and FC (Chen et al. 2016; Hong et al. 2014; Lenz et al. 2010). Similarly, in the current study for lodgepole pine, density showed a negative genetic correlation with RFW and TFW, while it showed a positive genetic
correlation with FWT, and FC. 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).

Microfibril angle (MFA) in Övra had a non-significant genetic correlation with fiber-dimension traits, except for its genetic correlation with TFW. A non-significant genetic correlation was also found between MFA and RFW in Lagfors. This suggests that future breeding programs of lodgepole pine, aiming at reduction of MFA and therefore improvement of modulus of elasticity (MOE), would have a negligible influence on fiber-dimension traits. Generally, a large sample size is needed for a precise estimation of genetic correlations with strong power (Klein 1974). In the current study, selection of four trees per family compared to other studies (5-12 trees) using SilviScan, might have caused higher standard errors than several reported studies (Chen et al 2014, Hong et al 2015). For future investigations, selection of more than four trees per family is desirable.

**Early selection efficiency**

Efficiency of early age selection of lodgepole pine fiber-dimension traits has not been examined before. Age-age genetic correlations from early rings to the reference ring (26 years) were very high in this study, as correlations reached unity around ring 5 at both trials. Generally, early selection efficiencies were higher in Lagfors, except for FWT, which was higher in Övra. This can be due to the higher age-age genetic correlation obtained for this trait at earlier ages in Övra, despite the fact that heritabilities of FWT at both trials were similar at this age. Higher early selection efficiencies found for RFW, TFW and FC in Lagfors can be attributed to the higher heritabilities obtained for these traits in Lagfors (Fig 2). Early selection efficiencies observed in Lagfors were similar to those reported by Hong et al. (2014) in Scots pine, as early selection after age 6 was as efficient as the reference age 26. Efficiencies in Övra reached unity after age 10, except for FWT, which was already highly efficient at age 3.

**Index selection and selection scenarios**

Breeding to improve stiffness in Swedish lodgepole pine populations is highly important, as the breakage and general instability of lodgepole pine due to a lower bending strength, or lower MOE of the stem has been a major issue (Fries et al. 2014), particularly in northern Sweden. However,
selection to improve stiffness alone might influence growth-related traits adversely, due to the
unfavourable genetic correlation between growth and wood quality traits (Hayatgheibi et al. 2017).

Index selection is an efficient method to improve several traits simultaneously, and the Smith-Hazel
index is by far one of the best-known methods of index selection, which takes account of economic
importance of objective traits (Cotterill and Dean 1990). Although determination of real economic
values is essential for the forestry enterprise, it is rarely done; therefore, alternative methods such as
Monte Carlo simulation (Dean et al. 1988), equal weight (Wu and Ying 1997), or desired gain
approach (Pesek and Baker 1969) are used (Ivkov’ic et al. 2006).

Similarly, the real economic weights for breeding-objective traits in lodgepole pine are not
defined yet. In this study, we constructed the default selection index combining MOE and diameter at
breast height (DBH) based on the economic weights suggested for Norway spruce (10 for MOE
relative to 1 for DBH, Chen et al. 2016).

Our results indicate that maximum genetic gains in combined selection of growth and stiffness
is achievable, when the selection index is constructed with the economical weighting of MOE ranging
from 7 to 10 relative to 1 for DBH. Additionally, we considered three different selection scenarios in
this study using a constant selection intensity of 1 % (Table 3). As expected from the observed genetic
 correlations (Table 2), selection for increased DBH alone (scenario A) would incur a negligible
decrease in density and slight increases in RFW, TFW, FC and FWT. Due to the negative genetic
correlation of MOE with RFW and its positive genetic correlation with FWT, FC, and density,
selection for increased MOE alone (scenario B) would cause a negligible reduction in RFW (-1.6 %)
and slight increases in FC (2.8%) , FWT (3.2%), and density (3.2 %). Genetic correlation of MOE
with TFW was negative in Övra while it was high and positive in Lagfors and correlations were
associated with large standard errors. As such, selection under scenario B, when trials are considered
jointly, would incur a negligible increase in TFW (0.9 %).

Combined selection of economically weighted DBH and MOE (scenario C) would cause slight
increases in density and all fiber properties. This finding is consistent with result of the study by Chen
et al. (2016) for Norway spruce, which has similarly shown combined selection of DBH and MOE (10
weights for MOE relative to 1 for DBH) would generate positive genetic gains in fiber properties.
Generally, scenario C was the most optimal selection as correlated genetic responses of all objective
traits were favourable under such selection. However, economical weights applied in this study were
those suggested for Norway spruce based on the economic breeding objectives developed for
production of radiata pine (Chen et al. 2016). In the future, in order to develop a more accurate
selection index, real economic weights based on the current lodgepole pine production system for both
solid-wood and pulp and paper products should be applied.

Conclusion
Phenotypic trends observed for fiber traits were generally similar at both trials. Age trends of
inheritance were lower near the pith and increased with cambial maturity until they stabilized near the
bark. Additionally, early selection for fiber-dimension traits was highly effective at age 5 years in
Lagfors and at age 8 years in Övra. Selection based on diameter at breast height (DBH) and modulus
of elasticity (MOE) alone will have unfavourable, but negligible, effects on wood density and radial
fiber width (RFW), and slightly favourable or no effects on the rest of fiber-dimension properties.
Combined selection of DBH and MOE in an index using economical weights, would cause positive
genetic gains in both traits.

Acknowledgement
The authors gratefully acknowledge financial support from Föreningen Skogsträdförädling, Bo
Rydins, Kempe foundations, and Swedish University of Agricultural Sciences (SLU). We would also
acknowledge Liming Bian, Zhiqiang Chen, David Hall and Zhou Hong for their assistance in field
sampling.
References


Cotterill, P.P., and Dean, C.A. 1990. Successful tree breeding with index selection. CSIRO, Melbourne, Australia.


Table 1. Mean, minimum to maximum range (Min–max), and phenotypic coefficient of variation ($CV_p$) for pith-to-bark core-wood properties in two lodgepole pine trials.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Trial</th>
<th>Övra (n=399)</th>
<th>Lagfors (n=424)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Min-max</td>
<td>CV (%)</td>
</tr>
<tr>
<td>Core length (mm)</td>
<td></td>
<td>136.1</td>
<td>72-218</td>
<td>18.49</td>
</tr>
<tr>
<td>DBH (mm)</td>
<td></td>
<td>130.5</td>
<td>30-232.5</td>
<td>24.47</td>
</tr>
<tr>
<td>Area-wt. Den (kg/m)</td>
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<td>456.6</td>
<td>365.8-582.1</td>
<td>8.11</td>
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<tr>
<td>Area-wt. RFW (µm)</td>
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<td>31.74</td>
<td>26.88-36.24</td>
<td>5.94</td>
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<tr>
<td>Area-wt. TFW (µm)</td>
<td></td>
<td>28.8</td>
<td>25.43-31.80</td>
<td>3.92</td>
</tr>
<tr>
<td>Area-wt. FWT (µm)</td>
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<td>2.45</td>
<td>1.98-3.05</td>
<td>7.76</td>
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<tr>
<td>Area-wt. FC (µg/m)</td>
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<td>397.7</td>
<td>300.3-516.9</td>
<td>8.01</td>
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<tr>
<td>Area-wt. MFA (°)</td>
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<td>18.6</td>
<td>8.20-36.41</td>
<td>27.89</td>
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<tr>
<td>Area-wt. MOE (Gpa)</td>
<td></td>
<td>10.42</td>
<td>4.66-17.50</td>
<td>20.99</td>
</tr>
</tbody>
</table>

Note: DBH diameter at breast height, Area-wt. area-weighted, DEN mean wood density, RFW radial fiber width, TFW tangential fiber width, FWT fiber wall thickness, FC fiber coarseness, MFA microfibril angle, MOE modulus of elasticity
Table 2. Additive genetic (above diagonal) and phenotypic (below diagonal) correlations among growth, area-weighted solid-wood and area-weighted fiber-dimension traits in two progeny trials of lodgepole pine. Narrow-sense heritability estimates of traits are shown on the diagonal of the table (Standard errors within the parentheses)

<table>
<thead>
<tr>
<th></th>
<th>DBH</th>
<th>Density</th>
<th>RFW</th>
<th>TFW</th>
<th>FWT</th>
<th>FC</th>
<th>MFA</th>
<th>MOE</th>
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</thead>
<tbody>
<tr>
<td>Övra</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DBH</td>
<td>0.10 (0.04)</td>
<td>-0.24 (0.23)</td>
<td>0.55 (0.14)</td>
<td>0.49 (0.17)</td>
<td>0.10 (0.21)</td>
<td>0.67 (0.27)</td>
<td>0.80 (0.61)</td>
<td>-0.51 (0.26)</td>
</tr>
<tr>
<td>Density</td>
<td>-0.26 (0.05)</td>
<td>0.29 (0.22)</td>
<td>-0.48 (0.17)</td>
<td>-0.71 (0.17)</td>
<td>0.90 (0.04)</td>
<td>0.39 (0.20)</td>
<td>0.04 (0.29)</td>
<td>0.65 (0.27)</td>
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<tr>
<td>RFW</td>
<td>0.53 (0.04)</td>
<td>-0.43 (0.04)</td>
<td>0.71 (0.21)</td>
<td>0.53 (0.17)</td>
<td>-0.14 (0.26)</td>
<td>0.55 (0.17)</td>
<td>0.04 (0.28)</td>
<td>-0.33 (0.28)</td>
</tr>
<tr>
<td>TFW</td>
<td>0.43 (0.04)</td>
<td>-0.48 (0.04)</td>
<td>0.46 (0.04)</td>
<td>0.44 (0.21)</td>
<td>-0.53 (0.27)</td>
<td>0.20 (0.25)</td>
<td>-0.19 (0.31)</td>
<td>-0.30 (0.31)</td>
</tr>
<tr>
<td>FWT</td>
<td>-0.01 (0.05)</td>
<td>0.89 (0.01)</td>
<td>-0.02 (0.05)</td>
<td>-0.13 (0.05)</td>
<td>0.29 (0.21)</td>
<td>0.78 (0.10)</td>
<td>0.04 (0.35)</td>
<td>0.66 (0.30)</td>
</tr>
<tr>
<td>FC</td>
<td>0.35 (0.04)</td>
<td>0.46 (0.04)</td>
<td>0.50 (0.04)</td>
<td>0.34 (0.04)</td>
<td>0.81 (0.02)</td>
<td>0.52 (0.21)</td>
<td>-0.01 (0.32)</td>
<td>0.28 (0.33)</td>
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<tr>
<td>MFA</td>
<td>0.19 (0.05)</td>
<td>0.06 (0.05)</td>
<td>-0.02 (0.05)</td>
<td>-0.10 (0.05)</td>
<td>0.04 (0.05)</td>
<td>0.02 (0.05)</td>
<td>0.30 (0.20)</td>
<td>-0.75 (0.18)</td>
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<tr>
<td>MOE</td>
<td>-0.28 (0.05)</td>
<td>-0.28 (0.05)</td>
<td>-0.16 (0.01)</td>
<td>-0.12 (0.05)</td>
<td>0.30 (0.05)</td>
<td>0.14 (0.01)</td>
<td>-0.88 (0.01)</td>
<td>0.30 (0.20)</td>
</tr>
<tr>
<td>Lagfors</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>DBH</td>
<td>0.12 (0.04)</td>
<td>-0.31 (0.22)</td>
<td>0.41 (0.13)</td>
<td>0.32 (0.15)</td>
<td>-0.03 (0.17)</td>
<td>0.28 (0.22)</td>
<td>0.35 (0.33)</td>
<td>-0.80 (0.54)</td>
</tr>
<tr>
<td>Density</td>
<td>-0.35 (0.04)</td>
<td>0.66 (0.21)</td>
<td>-0.31 (0.19)</td>
<td>-0.20 (0.21)</td>
<td>0.91 (0.04)</td>
<td>0.60 (0.14)</td>
<td>0.50 (0.33)</td>
<td>0.29 (0.35)</td>
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<tr>
<td>RFW</td>
<td>0.50 (0.04)</td>
<td>-0.37 (0.04)</td>
<td>0.73 (0.20)</td>
<td>0.20 (0.20)</td>
<td>0.03 (0.21)</td>
<td>0.45 (0.17)</td>
<td>-0.04 (0.28)</td>
<td>-0.08 (0.34)</td>
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<tr>
<td>TFW</td>
<td>0.52 (0.04)</td>
<td>-0.31 (0.05)</td>
<td>0.43 (0.04)</td>
<td>0.74 (0.20)</td>
<td>0.09 (0.22)</td>
<td>0.39 (0.18)</td>
<td>-0.56 (0.28)</td>
<td>0.58 (0.46)</td>
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<tr>
<td>FWT</td>
<td>-0.10 (0.05)</td>
<td>0.90 (0.00)</td>
<td>0.00 (0.05)</td>
<td>0.03 (0.05)</td>
<td>0.72 (0.21)</td>
<td>0.87 (0.05)</td>
<td>0.40 (0.33)</td>
<td>0.26 (0.40)</td>
</tr>
<tr>
<td>FC</td>
<td>0.25 (0.05)</td>
<td>0.55 (0.04)</td>
<td>0.46 (0.04)</td>
<td>0.43 (0.04)</td>
<td>0.85 (0.01)</td>
<td>0.72 (0.20)</td>
<td>0.30 (0.33)</td>
<td>0.39 (0.38)</td>
</tr>
<tr>
<td>MFA</td>
<td>0.23 (0.05)</td>
<td>-0.12 (0.05)</td>
<td>-0.04 (0.05)</td>
<td>-0.14 (0.05)</td>
<td>-0.18 (0.05)</td>
<td>-0.19 (0.05)</td>
<td>0.33 (0.19)</td>
<td>-0.68 (0.26)</td>
</tr>
<tr>
<td>MOE</td>
<td>-0.32 (0.05)</td>
<td>0.54 (0.03)</td>
<td>-0.11 (0.05)</td>
<td>-0.03 (0.05)</td>
<td>0.56 (0.03)</td>
<td>0.40 (0.04)</td>
<td>-0.87 (0.01)</td>
<td>0.13 (0.16)</td>
</tr>
</tbody>
</table>

Note: DBH diameter at breast height, Area-wt. area-weighted, RFW radial fiber width, TFW tangential fiber width, FWT fiber wall thickness, FC fiber coarseness, MFA microfibril angle, MOE modulus of elasticity
Table 3. Correlated genetic responses for area-weighted density, RFW, TFW, FWT and FC when different selection scenarios were used under a selection intensity of 1 % (i=2.67) (trials are considered jointly)

<table>
<thead>
<tr>
<th>Selection trait&lt;sup&gt;1)&lt;/sup&gt;</th>
<th>RFW</th>
<th>TFW</th>
<th>FWT</th>
<th>FC</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2.1</td>
<td>1.0</td>
<td>0.2</td>
<td>2.5</td>
<td>-1.5</td>
</tr>
<tr>
<td>B</td>
<td>-1.6</td>
<td>0.9</td>
<td>3.2</td>
<td>2.8</td>
<td>3.2</td>
</tr>
<tr>
<td>C</td>
<td>0.2</td>
<td>1.5</td>
<td>3.6</td>
<td>4.4</td>
<td>2.3</td>
</tr>
</tbody>
</table>

Note: RFW, radial fiber width; TFW, tangential fiber width; FWT, fiber wall thickness; FC, fiber coarseness

<sup>1)</sup>Selection trait: A, selection for increased diameter alone; B, selection for increased MOE alone; C, selection index combining DBH and MOE using economic weights (10 for MOE relative to 1 for DBH)
Figure Captions

Fig. 1 Phenotypic trends for mean a) radial fiber width b) tangential fiber width c) fiber wall thickness, and d) fiber wall coarseness from cambial age 1 to 26 at breast height for the two trials of lodgepole pine (Övra (n= 399) and Lagfors (n=424))

Fig. 2 Narrow-sense heritability trends for a) radial fiber width, b) tangential fiber width, c) fiber wall thickness, and d) fiber wall coarseness from cambial age 1 to 26 at breast height, based on cumulative area-weighted values, for the two trials of lodgepole pine

Fig. 3 Age-age genetic correlation between earlier ages and the reference age of 26 years in wood properties for a) radial fiber width b) tangential fiber width c) fiber wall thickness, and d) fiber wall coarseness from cambial age 1 to 26 at breast height, based on cumulative area-weighted values, for the two trials of lodgepole pine

Fig. 4 Efficiency of early selection between earlier ages and the reference age of 26 years in wood properties for a) radial fiber width b) tangential fiber width c) fiber wall thickness, and d) fiber wall coarseness from cambial age 1 to 26 at breast height, based on cumulative area-weighted values, for the two trials of lodgepole pine

Fig. 5 Expected genetic changes of diameter at breast height (DBH) (bold) and modulus of elasticity (MOE) to 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).
Fig. 1

(a) Radial fiber width

(b) Tangential fiber width

(c) Fiber wall thickness

(d) Fiber coarseness

Annual ring at breast height

Mean value (µm)

0 2 4 6 8 10 12 14 16 18 20 22 24

Mean value (µm)

0 2 4 6 8 10 12 14 16 18 20 22 24

Mean value (µg/m)

300 350 400 450 500

0 4 8 12 16 20 24

0 4 8 12 16 20 24

Annual ring at breast height

Ovra

Lagfors
Fig. 2

a) Radial fiber width

b) Tangential fiber width

c) Fiber wall thickness

d) Fiber coarseness
Fig. 3

a) Radial fiber width

b) Tangential fiber width

c) Fiber wall thickness

d) Fiber coarseness

Annual ring at breast height

Genetic correlation

Övra  Lagfors
Fig. 4

a) Radial fiber width

b) Tangential fiber width

c) Fiber wall thickness

d) Fiber coarseness

Selection efficiency

Annual ring at breast height

- Övra
- Lagfors

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Fig. 5

[Graph showing economic weights for MOE (Modulus of Elasticity) and DBH (Diameter at Breast Height)]