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ARTICLE

Genetic analysis of lodgepole pine (*Pinus contorta*) solid-wood quality traits

Haleh Hayatgheibi, Anders Fries, Johan Kroon, and Harry X. Wu

Abstract: Potential improvement of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) solid-wood properties was examined by estimating age trends of inheritance, age–age genetic correlations, and the efficiency of early selection using 823 increment cores sampled from 207 half-sib families at two independent progeny trials, aged 34–35 years, located in northern Sweden. High-resolution radial variation of annual ring width, wood density, microfibril angle (MFA), and modulus of elasticity (clearwood stiffness; MOE_S) was measured using SilviScan. The dynamic stiffness (MOE_{tof}) of standing trees was also obtained using Hitman ST300. Heritabilities ranged from 0.10 to 0.64 for growth and earlywood, transition-wood, and latewood proportions, from 0.29 to 0.77 for density traits, and from 0.13 to 0.33 for MFA and stiffness traits. Genetic correlations between early age and the reference age (26 years) suggested that early selection is efficient at age 4 years for MFA and between ages 5 to 8 years for density and MOE_S. Unfavorable diameter–stiffness genetic correlations and correlated responses indicate that breeding for a 1% increase in diameter would confer 5.5% and 2.3% decreases in lodgepole pine MOE_S and MOE_{tof}, respectively. Index selection with appropriate economical weights for growth and wood stiffness is highly recommended for selective breeding.

Key words: Pinus contorta, solid-wood properties, early selection, genetic parameters, genetic gain.

Résumé : Le potentiel d'amélioration des propriétés du bois massif chez le pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) a été étudié en estimant les tendances de l'héritabilité selon l'âge, les corrélations génétiques entre différents âges ainsi que l'efficacité de la sélection précoce. Pour ce faire, 823 carottes de bois ont été échantillonnées chez 207 descendances uniparentales établies dans deux tests de descendance indépendants âgés entre 34 et 35 ans et situés dans le nord de la Suède. L'utilisation de la technologie SilviScan a permis de mesurer à haute résolution la variation radiale de la largeur des cernes annuels, la densité du bois, l'angle des microfibrilles (AMF) et le module d'élasticité (la rigidité du bois sans défauts, MOE_S). La rigidité dynamique du bois (MOE_{tof}) des arbres debout a aussi été obtenue à l'aide du Hitman ST300. Les héritabilités variaient de 0,10 à 0,64 pour la croissance ainsi que pour les proportions de bois initial, de bois de transition et de bois final. Elles variaient de 0,29 à 0,77 pour les caractères de densité et de 0,13 à 0,33 pour l'AMF et les caractères de rigidité. Les corrélations génétiques entre l'âge précoce et l'âge de référence (26 ans) indiquent que la sélection précoce serait efficace dès l'âge de 4 ans pour l'AMF et entre l'âge de 5 et 8 ans pour la densité et le MOE_S. Des corrélations génétiques défavorables entre le diamètre et la rigidité, et des réponses corrélées indiquent que la sélection pour augmenter le diamètre de 1 % chez le pin tordu latifolié entraînerait des diminutions respectives de 5,5 et 2,3 % pour le MOE_S et le MOE_{tof}. La sélection sur indices avec des poids économiques appropriés pour la croissance et la rigidité du bois est fortement recommandée pour réaliser la sélection dirigée. [Traduit par la Rédaction]

Mots-clés : Pinus contorta, propriétés du bois massif, sélection précoce, paramètres génétiques, gain génétique.

Introduction

Lodgepole pine (*Pinus contorta* Doug. Ex Loud. var. *latifolia* Engelm.) is a major component of coniferous forests in North America (Critchfield 1980), spanning widely from Yukon territory to California through British Columbia and Alberta in western Canada and the USA (Critchfield 1957). In its natural habitat, lodgepole pine is ecologically a cornerstone species and renowned for its adaptation to harsh cold and dry conditions (Koch 1996). It is mainly used as sawtimber and pulpwood production in western Canada. Due to its high tolerance to a wide range of environments and its usable commercial products, it has been planted as an exotic species in many countries (Elfving et al. 2001) such as New Zealand (Ledgard 2001), Finland (Weissenberg 1972), Iceland (Sigurgeirsson 1988), and Sweden (Rosvall and Ericsson 1998).

In Sweden, early observations from small plantations of lodgepole pine between 1910 and 1930 indicated that this exotic species could be more productive than the native Scots pine (*Pinus sylvesteris* L.). The higher productivity has also been demonstrated in later studies in which 10-year-old lodgepole pine plus-trees were superior to Scots pine in terms of growth, survival, and damage resistance (Ericsson 1993). The productivity of lodgepole pine was estimated to be 36% higher than that of Scots pine under comparable conditions (Elfving and Norgren 1993). Large-scale provenance tests were conducted during the 1960s and 1970s to select the adaptive populations for systematic planting and alleviate the predicted future shortage of timber in Sweden (Hagner 1971, 1983; Nellbeck 1981). A Swedish project to secure materials for breeding and utilization of lodgepole pine was initiated in the

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1970s. Over 1000 plus-trees from 100 natural stands distributed in the interior of Yukon, British Columbia, and Alberta were selected as the base breeding materials, and open-pollinated seeds were collected from these selections (Bartram 1980; Ericsson 1993). Six preliminary breeding zones in northern Sweden were proposed based on latitude and elevation, mirroring similar climate regions and seed transfer zones in western Canada. Eighteen progeny trials were established in the 1980s as the first-generation progeny trials for selection of the next generation of breeding materials (Ericsson 1993).

To date, breeding materials for the second generation have been selected based mainly on growth, vitality, and adaptive traits. Several studies estimated genetic parameters of growth, survival, and form traits in Swedish lodgepole pine progeny trials (Ericsson and Danell 1995; Ericsson et al. 1994; Fries and Lindgren 1986). However, wood quality of lodgepole pine is a main issue in northern Sweden as there is a higher frequency of stem sweep and breakage compared with Scots pine (Hansson and Karlman 1997). This may be due to a larger foliage biomass (Norgren 1996), lower bending strength, or lower modulus of elasticity of the stem (Andersson 1987; Fries et al. 2014). The larger crown size and more elastic stem of lodgepole pine than Scots pine might be the cause of more instability of lodgepole pine trees under the wind and snow load. Therefore, improvement of wood stiffness and crown structure using genetics and silviculture is an important step for a successful implementation of lodgepole pine plantation forests.

Among many wood properties affecting the stiffness and other end-use products, wood density is the most studied trait for a wide range of species (Zobel and van Buijtenen 1989). Along with density, microfibril angle (MFA) has also been found to have a strong influence on stiffness (i.e., modulus of elasticity (MOE)) and strength of solid-wood products (Cave 1976; Evans et al. 2000; Fries et al. 2014). Nevertheless, genetic parameters of MFA have been less well studied compared with density owing to the difficulty in measuring this trait (Kennedy et al. 2013). Due to the great variation of MFA within annual rings (Brändström 2002), MFA of large numbers of tracheids are needed to be measured to characterize its properties adequately (Gräns et al. 2009). Development of the SilviScan technology (Evans 1994) has enabled high-resolution measurement of radial variation and age trend analysis of genetic parameters for many solid-wood properties in a wide range of species.

Several studies based on SilviScan measurement confirmed the influence of cambial age on inheritance and genetic control of wood properties and growth traits (Baltunis et al. 2007; Chen et al. 2014; Gräns et al. 2009; Hong et al. 2015; Lenz et al. 2010, 2011). Narrow-sense heritability estimates of density in such studies were usually greater than those of MOE and MFA, and growth traits had the lowest heritability estimates. Additionally, high age–age genetic correlations observed for different wood traits suggested possible gains from early selection of wood quality traits. Correlation between growth traits and wood properties were also reported for several conifer species. Nearly all estimated genetic correlations between density and growth traits were negative, particularly in radiata pine (*Pinus radiata* D. Don) (Baltunis et al. 2007; Gapare et al. 2009; Wu et al. 2008), Scots pine (Fries 2012; Hong et al. 2014), Norway spruce (*Picea abies* L. Karst.) (Chen et al. 2014), and white spruce (*Picea glauca* MoenchVoss.) (Lenz et al. 2011; Steffenrem et al. 2009). Due to such unfavorable correlation, it is of vital importance to investigate incorporation of wood quality traits as selection criteria in advanced breeding programs of lodgepole pine to ascertain that future end-use products have appropriate properties (Wu et al. 2007). To incorporate wood properties in lodgepole pine breeding program, genetic parameters such as age trends of heritability, genetic correlations, and optimal early age selection should be examined.

The main focus of this study was to assess genetic parameters of solid-wood traits, e.g., wood density, earlywood and latewood proportions, MFA, clear wood stiffness, and dynamic acoustic wood stiffness of standing trees of lodgepole pine in the Swedish progeny trials. Specific objectives were to (*i*) quantify genetic variation and inheritance for growth and wood quality traits, (*ii*) estimate genetic and phenotypic correlations between growth and wood quality traits, (*iii*) estimate age–age genetic correlation and efficiency of early selection, and (*iv*) evaluate possible genetic gain using different selection criteria.

Table 1. Description of the two lodgepole pine progeny trials and sampling details for growth and wood quality traits.

	Trial	
	Övra	Lagfors
Latitude	63°57′N	62°45′N
Longitude	16°46′E	17°08′E
Elevation (m)	350	220
Annual rainfall (mm)	669	677
Soil type	Sandy–silty moraine	Sandy moraine
Planting year	1980	1979
Breeding zone	4	5
No. of provenances	4	2
Total no. of families	178	214
Total no. of sampled trees and families for DBH	4329–178	6289–214
Total no. of sampled trees and families for AV	1250–100	1332–115
Total no. of sampled trees and families for SilviScan	399–100	424–107

Note: DBH, diameter at breast height; AV, acoustic velocity.

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 selected for this study. Trial and sampling details are presented in Table 1. Övra was planted in 1980 with 178 open-pollinated families originating from four geographic regions (provenances) (Fort Nelson, Watson Lake, Fort St. John, and Prince George). Lagfors was planted in 1979 with 214 open-pollinated families originating from two provenances (Fort St. John and Prince George). There were no common families between the two trials. These families at both trials were planted in a randomized complete block (RCB) design. Each family was represented by 10 trees planted in a row with five replicates, resulting in 50 planted trees per family. Tree spacing was 2 m between rows and 1.5 m within rows. Bark-to-bark increment cores were sampled and acoustic velocity (AV) on standing tree was measured in the summer of 2014, 34 and 35 years after planting, in Övra and Lagfors, respectively. A complete assessment of diameter at breast height (DBH), vitality, damages, and general condition (i.e., double stem) was made on 4329 trees at Övra and on 6289 trees at Lagfors, aged 34 and 36 years, respectively. Double stem was scored as 1 for trees with a double stem below their breast height (1.3 m) and 0 otherwise. A total of 399 trees were sampled at Övra, at age 34 years (approximately four trees from 100 families), and 424 trees, at age 35 years (approximately four trees from 107 families), were sampled at Lagfors.

SilviScan measurement

A total of 399 trees were sampled at Övra (approximately four trees from 100 families), while 424 trees (approximately four trees from 107 families) were sampled at Lagfors. Bark-to-bark increment cores (12 mm in diameter) were collected at breast height from these 823 trees using an electronic boring machine and assessed by SilviScan instruments (Innventia AB, Stockholm, Sweden). As the orientation of family rows differed at the two trials, samples were collected from the northern face of trees in Övra, while they were collected from eastern face of trees in Lagfors. Before the SilviScan measurement, each increment core was sawn into a 7 mm high × 2mm thick radial strip from the pith to the bark. Each sample was soaked in clean acetone to remove extractives causing disturbances of the measurement. Samples were air-dried overnight in the laboratory at approximately 23 °C and 43% relative humidity. The SilviScan system combines image analysis with X-ray absorption and X-ray diffraction to determine a high-resolution pith-to-bark radial variation for several important wood properties such as wood density, MFA, and MOE (Evans 2006).

Density was obtained as an average for 25 μm radial intervals, while MFA was averaged over 2 mm intervals, and these estimates were used to predict MOE (Evans 2006). The widths and the average wood density, MFA, and MOE for each annual ring were determined. The three ring segments, earlywood (EW), transition wood (TW), and latewood (LW), were identified from the wood density variation within each ring as follows: EW was defined as the part of the ring with wood density that is 0%–20% of the span from minimum to maximum within the ring, LW is the wood in the 80%–100% span, and TW is the wood in the 20%–80% span. Based on these segments, earlywood density (EWD), transition-wood density (TWD), and latewood density (LWD) were identified. Proportions of earlywood width (EWP), transition-wood width (TWP), and latewood width (LWP) were also calculated. The cambial age at ring 26 (26 years) was used as a mature reference age, as most wood strips contained effective measurements for wood traits at cambial age 26.

The variation of wood properties from the SilviScan measurement was analysed for each annual ring and at the whole-core level. Because area-weighted values (AWV) more accurately represent the average properties of the wood (Gräns et al. 2009), the AWV for each trait was calculated and used in this study as follows:

$$\text{(1)} \qquad \text{AWV} = \frac{\Sigma(\alpha_i d_i)}{\Sigma \alpha_i}$$

where α_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).

Acoustic velocity measurement

Totals of 1250 trees from 100 families at Övra and 1332 trees from 115 families at Lagfors were selected to measure dynamic MOE of lodgepole pine. The Hitman ST300 tool (Fiber-gen, Christchurch, New Zealand) was used to measure the acoustic velocity (AV) of standing trees by inserting two sensor probes (transmitter and receiver) into the outer wood of the tree, with the lowest probe at around 1 m high. Probes were placed in sections of stem that had fewer branches and were vertically aligned at a distance of about 70 to 110 cm apart. The distance was measured with a laser beam, and an acoustic wave was passed through the stem by striking the transmitter probe with a steel hammer. The wave was picked up by the receiver probe and its time of flight (tof) was recorded. Two series of eight hits were taken per tree, and an average of two measurements was taken. Dynamic MOE (MOE_{tof}) can be estimated using the AV according to the Young's equation (Wang et al. 2001):

$$\text{(2)} \qquad \text{MOE} = \rho V^2$$

where ρ is the green density (kg·m^{-3}) (Bucur 2006) and V is the velocity of the wave (m·s^{-1}). A constant green density of 1000 kg·m^{-3} is normally used for calculating dynamic MOE in standing trees (Lenz et al. 2013).

Statistical analysis

All of the wood properties (density, MOE, MFA) and growth traits (DBH, ring width, EWP, TWP, and LWP) were analyzed in the ASReml statistical software package (Gilmour et al. 2009) using a linear mixed-effects model for individual sites. Additionally, bivariate analyses were used to estimate the genetic correlation between traits. The following model was used to estimate variance and covariance components for genetic parameters:

$$\text{(3)} \qquad \boldsymbol{y}_{jklm} = \mu + P_k + B_j + F_{l(k)} + BF_{jl(k)} + e_{jklms}$$

where $\boldsymbol{y}$ is the vector of observations on tree m from family l within provenance k in block j, μ is the overall mean, and P_k and B_j are the fixed effects of provenance k and block j, respectively. The variable $F_{l(k)}$ is the random effect of family l within provenance k, $BF_{jl(k)}$ is the random interactive effect of block j and family l within provenance k, and e_{jklm} is the random residual effect. To examine the effect of the double stem on the DBH trait, this variable was included in the model as a fixed effect of the double-stem covariate when it was significant at $\alpha = 0.05$.

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_i^2) for each trait at each trial was calculated using the following equation assuming that these open-pollinated families are half-sib families (Falconer and Mackay 1996):

$$\text{(4)} \qquad h_i^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} = \frac{4 \times \hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{bf}^2 + \hat{\sigma}_e^2}$$

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

$$\text{(5)} \qquad r_{(x,y)} = \frac{\widehat{\text{Cov}_{(x,y)}}}{\sqrt{\hat{\sigma}_{(x)}^2 \times \hat{\sigma}_{(y)}^2}}$$

where $\widehat{\text{Cov}_{(x,y)}}$ is the estimated phenotypic or genetic covariance between traits x and y or between early age and reference age (ring 26), $\hat{\sigma}_{(x)}^2$ is the estimated additive genetic variance for trait x or for early age, and $\hat{\sigma}_{(y)}^2$ 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

$$\text{(6)} \qquad E_{\text{gen}} = r_A \frac{i_E h_E}{i_A h_A}$$

where i_E is the selection intensity at the early age, i_A is the selection intensity at the reference age, h_E is the square root of heritability at the early age, h_A is the square root of heritability at the reference age, and r_A is the additive genetic correlation between early age and reference age. The same selection intensity for early age and reference age was used in this calculation. In the lodgepole pine breeding program, wood stiffness and growth are the main breeding objective traits. Therefore, genetic gains (G_i) were calculated to improve growth and stiffness traits (DBH, MOE_S, and MOE_{tof}) by direct selection and indirect selection using correlated

Table 2. 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.

	Trial					
	Övra			Lagfors		
Variables	Mean	Min–max	CV_p (%)	Mean	Min–max	CV_p (%)
Core length (mm)	136.1	72–218	18.49	125.6	77–205	15.5
DBH (mm)	130.5	30–232.5	24.47	128.1	40–250	21.65
Ring width (mm)	2.47	1.39–4.43	18.12	2.42	1.57–3.69	15.1
EWP (%)	51.79	31.23–68.07	10.5	50.66	38.42–64.78	8.48
TWP (%)	30.83	20.32–50.4	15.57	29.44	20.06–40.65	11.84
LWP (%)	17.38	9.84–28.09	16.55	19.9	12.73–28.67	14.01
DEN (kg·m^{-3})	456.6	365.8–582.1	8.11	483.2	385.9–570.7	6.98
EWD (kg·m^{-3})	343.2	286.6–431.6	7.19	357.2	279.2–426.9	6.14
TWD (kg·m^{-3})	499.8	409.6–591.2	6.75	520.2	431.5–612.8	5.87
LWD (kg·m^{-3})	735.8	603.7–870.2	6.9	774.4	632.6–914.3	6.32
MOE_S (GPa)	10.42	4.66–17.50	20.99	11.96	6.83–16.75	15.71
MFA (°)	18.6	8.20–36.41	27.89	16.62	8.20–29.40	23.8
MOE_{tof} (GPa)	13.69	5.53–21	17.11	15.93	9.22–25.64	15.08

Note: DBH, diameter at breast height; EWP, earlywood width proportion; TWP, transition-wood width proportion; LWP, latewood width proportion; DEN, area-weighted mean wood density; EWD, area-weighted earlywood density; TWD, area-weighted transition-wood density; LWD, area-weighted latewood density; MFA, microfibril angle; MOE_S, modulus of elasticity estimated using SilviScan; MOE_{tof}, modulus of elasticity estimated using acoustic velocity and constant green density.

traits. The genetic gain (expressed as percentage) in direct selection of trait *i* was estimated as

$$\Delta G_i = i \times h_i^2 \times CV_i \quad (7)$$

where *i* is the selection intensity of 1% (i = 2.67), h_i^2 is the narrow-sense heritability of the trait, and CV is the coefficient of variation of the phenotypic effect (calculated as the phenotypic standard deviation divided by the mean of the specific trait). The correlated response of the target trait *t* based on indirect selection of correlated trait *i* was calculated as

$$CR_t = i \times h_i \times h_t \times r_A \times CV_t \quad (8)$$

where *i* is the selection intensity of 1% (i = 2.667), h_i 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 trend for growth and wood quality traits

Trees in Övra grew faster and had higher MFA than those in Lagfors. In contrast, area-weighted wood densities, MOE_S, and MOE_{tof} were higher in Lagfors (Table 2). Trees originating from Watson Lake provenance had the highest density, while trees originating from Fort Nelson provenance had the lowest density in Övra. Results showed that the geographic region was a highly significant source of variation of wood density (P < 0.001) in Övra, whereas it was nonsignificant in Lagfors. Overall age trends for growth and wood quality traits were approximately similar at both trials (Fig. 1). Age trends of ring width at both trials peaked about annual ring 5, then declined towards the bark, and stabilized at about ring 19. Density at early ages changed little but increased from about ring 8 to ring 18 in Övra and to ring 19 in Lagfors and then stabilized towards the bark. However, density was greater in Lagfors after ring 11. MFA gradually dropped from 40° at ring 1 to about cambial age of 18 years for both trials and then stabilized at 13° and 10° towards the bark in Övra and Lagfors, respectively. In contrast, MOE increased from about 3 GPa for both trials to about 13 and 17 GPa close to the bark in Övra and Lagfors, respectively. Övra showed a slow decrease in MOE and increase in MFA moving from ring 12 towards the bark.

The proportion of latewood continuously increased from early age to the reference age of 26 years, while the proportion of earlywood increased initially and then declined after the cambial age of 14 years. Coefficients of variation (CV) varied from 6.8% to 27.9% in Övra and from 5.9% to 23.8% in Lagfors (Table 2). Among the growth traits, DBH had the greatest CV (24.5% in Övra and 21.7% in Lagfors) and earlywood proportion had the lowest CV (10.5% in Övra and 8.5% in Lagfors). Density traits had the lowest CV (6.9% to 8.11% in Övra and 5.9% to 7.0% in Lagfors), whereas MOE (21% in Övra and 15.8% in Lagfors) and MFA (27.9% in Övra and 23.8% in Lagfors) had the greatest CV.

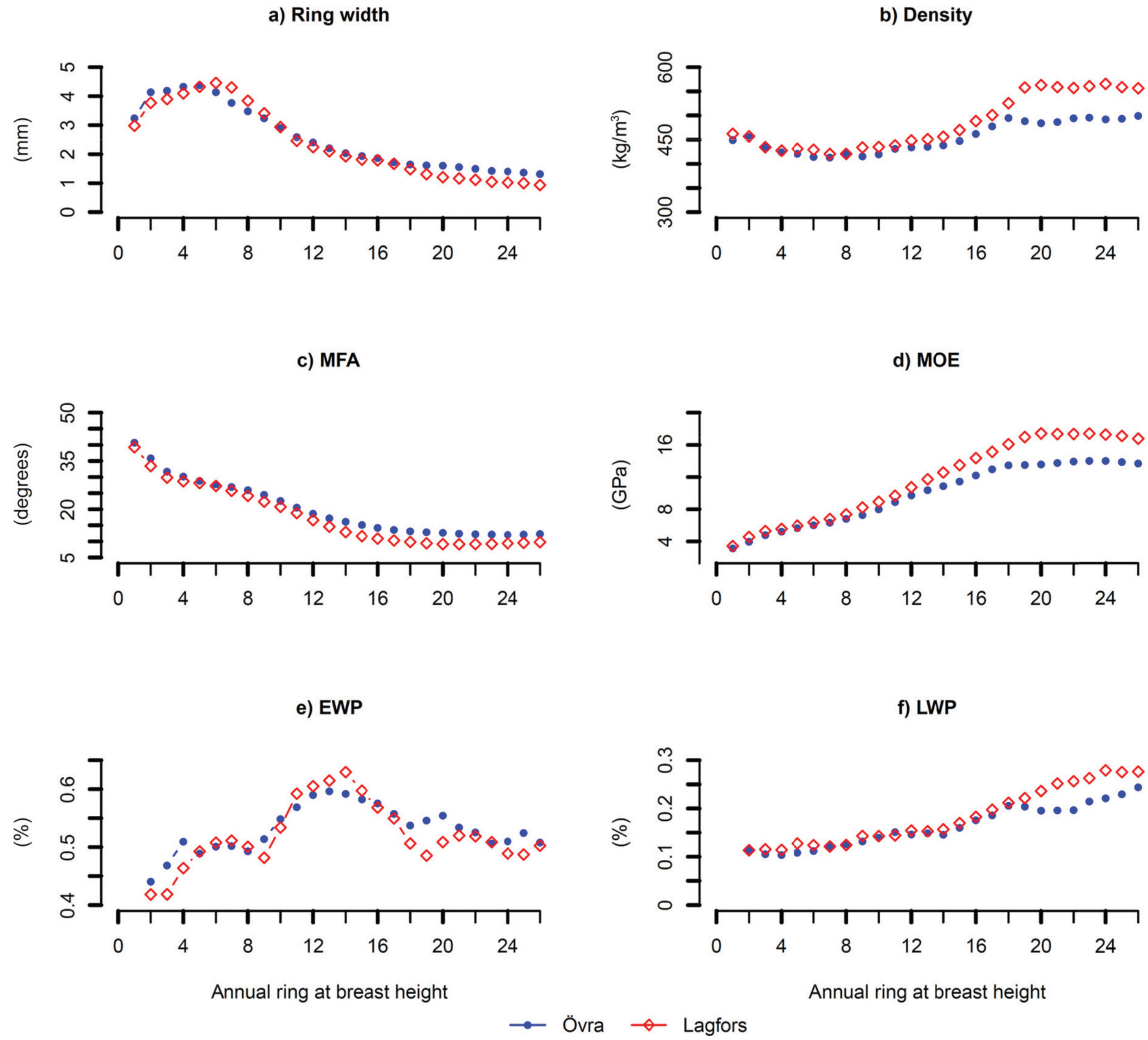
Trend for heritability

Narrow-sense individual heritability estimates obtained from cumulative ring width, area-weighted wood density, MOE, and MFA from annual ring 1 to annual ring 26 are presented in Fig. 2. Heritability of ring width in Övra increased steadily from a very low value near the pith and stabilized at around 0.3 towards the bark. In contrast, heritability of ring width in Lagfors was greater near the pith (around 0.4 from ring 1 to ring 6) and then decreased continuously to about zero after ring 20 towards the bark. Heritability for density fluctuated during the first three years near the pith in both trials and then increased to the cambial age of 10 years with a peak of 0.6 in Övra and 0.9 in Lagfors. After that, the heritability declined towards the bark. Heritability for MFA in Lagfors was greater than in Övra near the pith but converged to about 0.4 after the cambial age 8 at both trials. Heritability for MOE in Övra increased from 0.2 near the pith to 0.4 at ring 14, with some decrease towards the bark after age 20 years, whereas heritability for MOE in Lagfors was greater near the pith (around 0.5 from ring 2 to ring 6) and then declined steadily and stabilized to 0.2 towards the bark.

Correlations between growth traits and wood quality traits

Genetic and phenotypic correlations calculated for growth, area-weighted wood density, MFA, and stiffness traits are presented in Table 3. Genetic and phenotypic correlations between pairs of traits were similar at both trials, except for the genetic correlation of MFA with wood density and growth traits. For instance, in Övra, most genetic correlations were low positive or negative between MFA and wood density traits, whereas such correlations were pos-

Fig. 1. Phenotypic trends for mean (*a*) ring width, (*b*) wood density, (*c*) MFA, (*d*) MOE, (*e*) earlywood proportion (EWP), and (*f*) latewood proportion (LWP) from cambial age 1 to age 26 at breast height for two trials of lodgepole pine. [Colour online.]



itive in Lagfors (0.50, 0.61, 0.54, and 0.25 for density, EWD, TWD, and LWD, respectively). Genetic correlations for MFA with EWP, TWP, and LWP were greater in Lagfors than in Övra. Likewise, genetic correlations of MOE_S with EWP, TWP, and LWP differed considerably between the two trials.

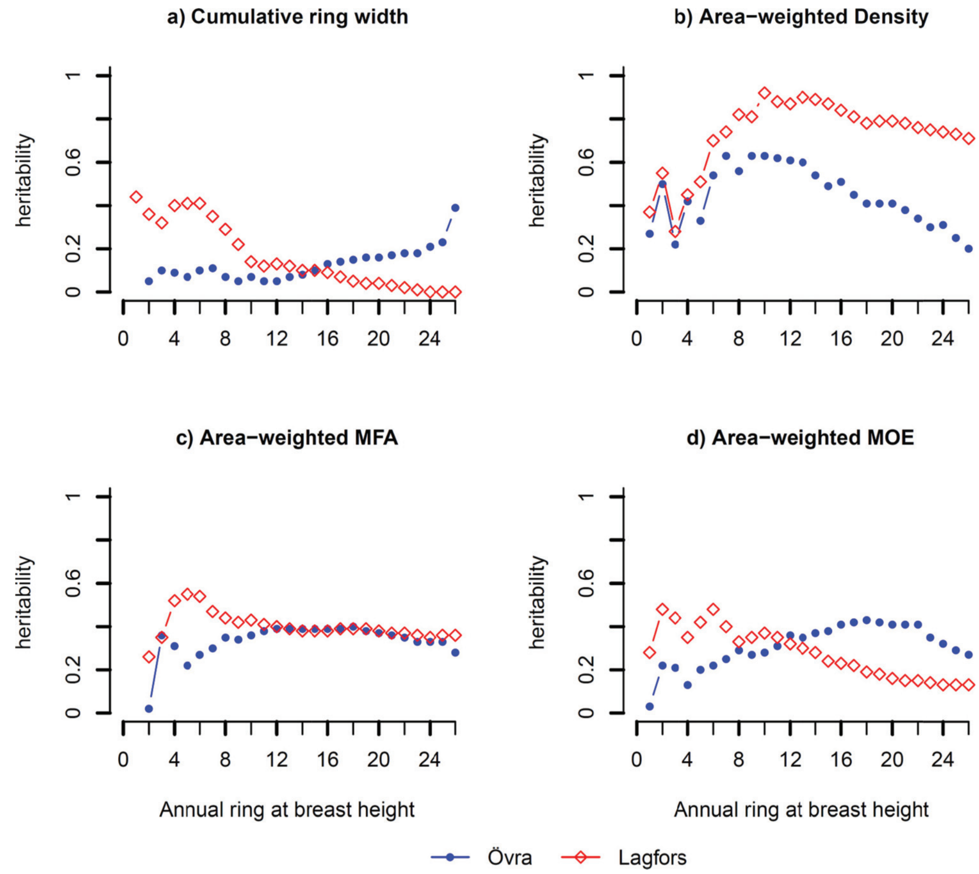
As expected, there were high positive genetic correlations among the four wood density traits at both trials. Furthermore, genetic correlation between the two stiffness measurements (MOE_S and MOE_{tof}) was high (0.91 and 0.90 in Övra and Lagfors, respectively), and stiffness had high and positive correlations with wood density traits at both trials. Similarly, stiffness had moderate to high negative genetic correlations with MFA (−0.75 and −0.67 in Övra and −0.68 and −0.43 in Lagfors for MOE_S and MOE_{tof}, respectively).

Genetic correlations of DBH with wood density and stiffness (MOE_S and MOE_{tof}) were negative at both trials. Genetic correlations of DBH with wood density traits ranged from −0.06 to −0.53 in Övra, while they varied from −0.31 to −0.68 in Lagfors. In Övra, genetic correlations between DBH and stiffness traits varied from −0.35 to −0.51, while they varied from −0.14 to −0.80 in Lagfors. In general, DBH had greater negative genetic correlations with wood density and MOE_S in Lagfors. Genetic correlations of EWP with all wood density and stiffness traits were negative at both trials except for genetic correlations of EWP with both LWD and MOE_S in Lagfors. Genetic correlations of TWP with density traits were low to moderate positive except for correlations with LWD, which were low to moderate negative at both trials. Similarly, genetic correlations of LWP with all density traits were moderate to high positive at both trials. Standard errors of genetic correlations with other traits were relatively large at both trials, particularly for correlations involving MFA and MOE_S. This might be due to small sample size of each family.

Age–age correlation

Age–age genetic correlations between each of the rings and the reference ring at age 26 years were calculated for cumulative ring width, wood density, MOE, and MFA (Fig. 3). The age–age genetic correlations were very high and reached 0.9 from ring 8 onwards for all studied traits at both trials. The age–age genetic correlations at earlier ages were higher in Lagfors for cumulative ring width, whereas they were lower for wood density and MFA. The genetic correlations of ring width were unusually high in Lagfors, above 0.8 from ring 1, while they reached 0.8 at ring 4 in Övra. For wood density in Lagfors, the genetic correlations reached 0.8 at ring 6, while they were around 0.8 already from ring 1 in Övra. The age–age genetic correlations for MOE and MFA were very similar

Fig. 2. Narrow-sense heritability trends for (*a*) cumulative ring width, (*b*) wood density, (*c*) MFA, and (*d*) MOE from cambial age 1 to age 26 at breast height, based on area-weighted values, for the two trials of lodgepole pine. [Colour online.]



at both trials, and MFA had the highest genetic correlations at earlier ages among the wood quality traits at both trials.

Early selection efficiency

Efficiency of early selection relative to selection based on the reference ring 26 calculated for cumulative ring width, area-weighted wood density, MOE, and MFA is shown in Fig. 4. Early selection efficiency for ring width in Övra was low from ring 1 and increased steadily towards the bark until it reached around 0.8 at the reference ring 26. Such efficiency was calculated only for Övra as the heritability of ring width in Lagfors was very low and reached zero at the reference ring 26. Early selection efficiency was very high for wood density, MFA, and MOE. Early selection efficiency for wood density was greater at Övra than in Lagfors, as efficiency in Övra reached 1 from the first rings, while such efficiency was achieved at ring 10 in Lagfors. This is mainly due to the higher age–age genetic correlation at early ages in Övra. Early selection for MFA was already at age 3 as efficient as selection at the reference ring 26 at both trials. Early selection efficiency for MOE was greater at earlier ages in Lagfors, peaking to higher than 1.5 at about ring 10 and then declining gradually and stabilizing to around 1 towards the bark. Such efficiency in Övra was very low at earlier ages, then increased steadily, and reached 1 at about ring 10. This is mainly due to the lower heritability at earlier ages in Övra.

Genetic gains and response to selection

Combined-site genetic gains (ΔG) from the direct selection on three breeding objective traits (DBH, MOE_S, and MOE_{tof}) and correlated genetic gains (CR_t) from the indirect selection based on growth and wood stiffness traits with a 1% selection intensity ($i = 2.67$) are presented in Table 4. The genetic gains observed for direct traits were moderate (e.g., ΔG_{DBH} = 7.9%, ΔG_{MOE_s} = 13%, and $\Delta G_{MOE_{tof}}$ = 12.7%). As expected, due to the negative genetic correlation of growth with MOE_S and MOE_{tof}, selection based on DBH generated negative genetic gains for MOE_S (–5.5%) and MOE_{tof} (–2.3%). Similarly, due to the negative genetic correlation of MFA with MOE_S and MOE_{tof}, selection for reduced MFA resulted in correlated responses for higher MOE_S (9.6%) and MOE_{tof} (8.0%).

Discussion

Similar to other early conifer breeding programs, wood quality traits were not included as selection criteria or breeding objective traits in the first-generation selection of Swedish lodgepole pine breeding programs (Ericsson and Danell 1995; Wu et al. 2008). In northern Sweden, improvement of wood properties is even more urgent, mainly due to the impact of snow pressure, which causes stem bending and stem breakage (Fries et al. 2014). Genetic parameters for wood quality traits have not been previously estimated for lodgepole pine. The focus of this study was mainly to evaluate the degree of genetic control for important solid-wood properties such as wood density, MFA, and MOE from pith to bark at two genetically independent progeny trials of lodgepole pine in Sweden. Most wood properties and their genetic controls change with cambial age and stabilize only with cambial maturity (Hannrup and Ekberg 1998; Lenz et al. 2010). In general, wood density and MOE increase and MFA decreases as trees become older, and such changes ensure that end-use products have desirable wood characteristics (Dungey et al. 2006). Higher MFA and lower MOE in rings near the pith were hypothesized to ensure flexibility of young stems and protect them from wind damage (Hong et al. 2015; Lenz et al. 2010).

Table 3. Additive genetic (above diagonal) and phenotypic (below diagonal) correlations between growth and area-weighted wood quality traits in two progeny trials of lodgepole pine.

	Growth traits				Wood quality traits						
	DBH	EWP	TWP	LWP	DEN	EWD	TWD	LWD	MFA	MOE_S	MOE_{tof}
Övra											
DBH	0.10 (0.04)	−0.36 (0.23)	0.67 (0.18)	−0.37 (0.15)	−0.24 (0.23)	−0.53 (0.25)	−0.14 (0.24)	−0.06 (0.25)	0.80 (0.61)	−0.51 (0.26)	−0.35 (0.20)
EWP	−0.09 (0.05)	0.17 (0.20)	−0.72 (0.15)	−0.32 (0.27)	−0.67 (0.18)	−0.60 (0.24)	−0.46 (0.26)	−0.28 (0.32)	−0.18 (0.35)	−0.42 (0.48)	−0.45 (0.29)
TWP	0.41 (0.04)	−0.85 (0.01)	0.47 (0.21)	−0.32 (0.24)	0.15 (0.24)	0.24 (0.25)	0.02 (0.25)	−0.12 (0.26)	0.07 (0.33)	0.05 (0.38)	0.30 (0.25)
LWP	−0.50 (0.04)	−0.48 (0.04)	−0.07 (0.05)	0.40 (0.22)	0.71 (0.12)	0.48 (0.18)	0.55 (0.17)	0.48 (0.20)	0.14 (0.29)	0.43 (0.26)	0.26 (0.28)
DEN	−0.26 (0.05)	−0.50 (0.04)	0.20 (0.05)	0.62 (0.03)	0.29 (0.22)	0.89 (0.05)	0.99 (0.03)	0.90 (0.09)	0.04 (0.29)	0.65 (0.27)	0.46 (0.25)
EWD	−0.29 (0.05)	−0.33 (0.04)	0.11 (0.05)	0.43 (0.04)	0.87 (0.01)	0.33 (0.22)	0.92 (0.08)	0.63 (0.17)	0.07 (0.31)	0.51 (0.29)	0.42 (0.28)
TWD	−0.17 (0.05)	−0.24 (0.05)	0.04 (0.05)	0.38 (0.04)	0.90 (0.01)	0.77 (0.02)	0.42 (0.23)	0.96 (0.04)	−0.02 (0.30)	0.67 (0.29)	0.36 (0.26)
LWD	−0.17 (0.05)	0.02 (0.05)	−0.18 (0.05)	0.26 (0.05)	0.75 (0.02)	0.59 (0.03)	0.87 (0.01)	0.40 (0.23)	−0.04 (0.30)	0.52 (0.25)	0.23 (0.27)
MFA	0.19 (0.05)	−0.40 (0.04)	0.48 (0.04)	−0.05 (0.05)	0.06 (0.05)	0.03 (0.05)	0.03 (0.05)	−0.16 (0.05)	0.30 (0.20)	−0.75 (0.16)	−0.67 (0.28)
MOE_S	−0.28 (0.05)	0.17 (0.05)	−0.37 (0.04)	0.31 (0.05)	0.34 (0.04)	0.32 (0.05)	0.32 (0.04)	0.45 (0.04)	−0.88 (0.01)	0.30 (0.20)	0.91 (0.30)
MOE_{tof}	−0.20 (0.03)	0.03 (0.05)	−0.15 (0.05)	0.20 (0.05)	0.25 (0.05)	0.24 (0.05)	0.21 (0.05)	0.24 (0.05)	−0.59 (0.03)	0.67 (0.03)	0.20 (0.09)
Lagfors											
DBH	0.12 (0.04)	−0.34 (0.17)	0.45 (0.17)	0.03 (0.19)	−0.31 (0.22)	−0.48 (0.20)	−0.49 (0.26)	−0.68 (0.22)	0.35 (0.33)	−0.80 (0.53)	−0.14 (0.20)
EWP	−0.03 (0.05)	0.64 (0.21)	−0.93 (0.15)	−0.97 (0.22)	−0.63 (0.15)	−0.43 (0.18)	−0.41 (0.23)	0.05 (0.25)	−0.96 (0.22)	0.55 (0.52)	−0.34 (0.18)
TWP	0.41 (0.04)	−0.76 (0.02)	0.30 (0.20)	0.39 (0.34)	0.44 (0.27)	0.39 (0.28)	0.14 (0.33)	−0.31 (0.33)	0.67 (0.27)	−0.37 (0.46)	0.33 (0.23)
LWP	−0.47 (0.04)	−0.57 (0.03)	−0.07 (0.05)	0.48 (0.21)	0.73 (0.16)	0.35 (0.21)	0.62 (0.23)	0.21 (0.29)	0.90 (0.37)	−0.26 (0.56)	0.28 (0.28)
DEN	−0.35 (0.04)	−0.49 (0.04)	0.09 (0.05)	0.63 (0.03)	0.66 (0.21)	0.94 (0.04)	0.96 (0.03)	0.73 (0.11)	0.50 (0.33)	0.29 (0.35)	0.62 (0.17)
EWD	−0.42 (0.04)	−0.27 (0.05)	0.00 (0.05)	0.42 (0.04)	0.87 (0.01)	0.76 (0.22)	0.93 (0.06)	0.76 (0.13)	0.61 (0.38)	0.39 (0.32)	0.56 (0.18)
TWD	−0.24 (0.05)	−0.23 (0.05)	−0.03 (0.05)	0.38 (0.04)	0.90 (0.00)	0.81 (0.02)	0.46 (0.20)	0.88 (0.07)	0.54 (0.44)	0.47 (0.36)	0.65 (0.21)
LWD	−0.35 (0.04)	0.03 (0.05)	−0.25 (0.04)	0.28 (0.04)	0.78 (0.02)	0.66 (0.03)	0.86 (0.01)	0.39 (0.20)	0.25 (0.43)	0.53 (0.32)	0.49 (0.21)
MFA	0.19 (0.05)	−0.33 (0.04)	0.40 (0.04)	0.00 (0.00)	−0.12 (0.05)	−0.13 (0.05)	−0.18 (0.05)	−0.37 (0.04)	0.33 (0.19)	−0.68 (0.26)	−0.43 (0.25)
MOE_S	−0.32 (0.05)	0.06 (0.05)	−0.30 (0.04)	0.28 (0.04)	0.54 (0.03)	0.49 (0.04)	0.53 (0.03)	0.64 (0.03)	−0.87 (0.01)	0.13 (0.16)	0.90 (0.30)
MOE_{tof}	−0.05 (0.03)	−0.12 (0.05)	−0.05 (0.05)	0.24 (0.04)	0.43 (0.04)	0.38 (0.04)	0.40 (0.04)	0.39 (0.04)	−0.46 (0.04)	0.61 (0.03)	0.29 (0.10)

Note: Narrow-sense heritability estimates of traits are shown on the diagonal (shaded) of the table (standard errors within the parentheses). DBH, diameter at breast height; EWP, earlywood width proportion; TWP, transition-wood width proportion; LWP, latewood width proportion; DEN, area-weighted mean wood density; EWD, area-weighted earlywood density; TWD, area-weighted transition-wood density; LWD, area-weighted latewood density; MFA, microfibril angle; MOE_S, modulus of elasticity estimated using SilviScan; MOE_{tof}, modulus of elasticity estimated using acoustic velocity and constant green density.

Mean values and site effect

Phenotypic trends observed for solid-wood properties in this study were similar to those of other conifers such as radiata pine (Dungey et al. 2006; Wu et al. 2007), Scots pine (Hong et al. 2015), Norway spruce (Chen et al. 2014; Gräns et al. 2009) and black spruce (*Picea mariana* (Mill.) BSP) (Alteyrac et al. 2007). Density and MOE were higher, while MFA was lower in rings near the pith, then density and MOE increased, while MFA decreased, and all properties stabilized with cambial maturity at both trials. The age trends observed for ring density were also consistent with previous reports in lodgepole pine as annual ring density dropped initially to a minimum in rings 6 to 10 and then increased to a maximum towards the bark (Taylor et al. 2007). Phenotypic trends observed for density and LWP were similar, as both traits increased steadily from the pith towards the bark.

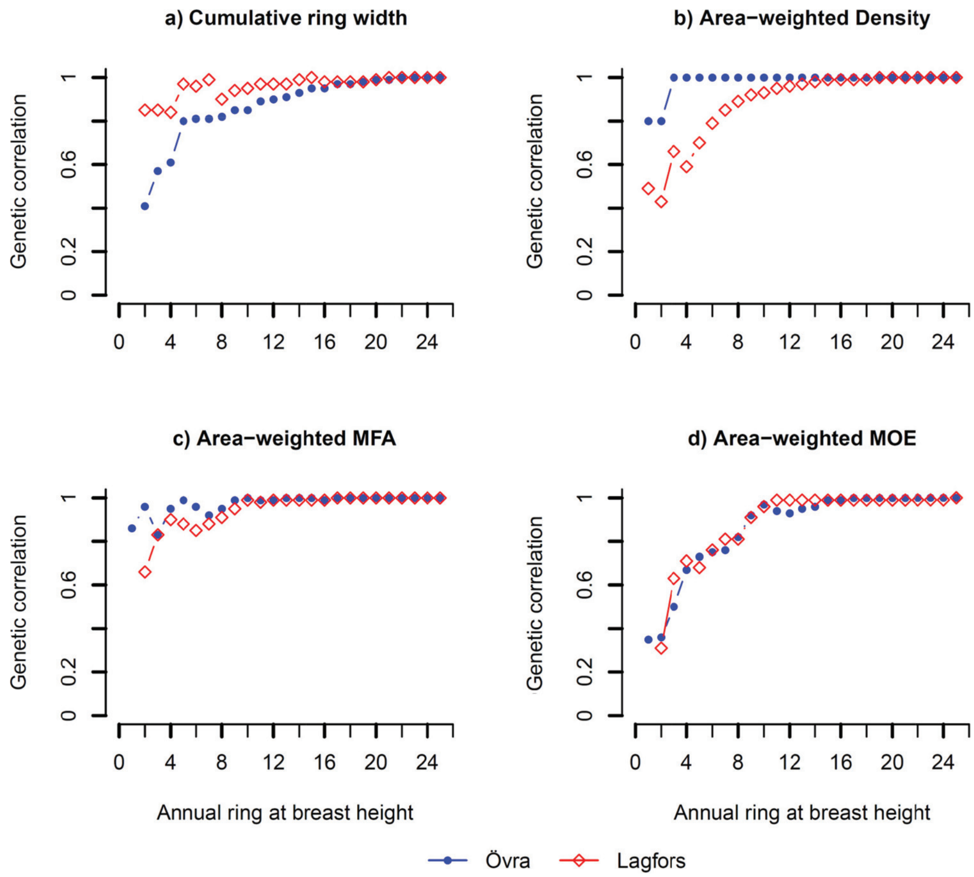
Observations of relationships between growth and wood properties among sites usually indicate that the site of higher fertility (higher growth rate) produces trees with lower wood density and lower stiffness (Baltunis et al. 2007; Wu et al. 2007; Gapare et al. 2009; Chen et al. 2014). The two progeny trials investigated in this study were genetically different; however, their phenotypic trends observed for most traits were generally identical. Density, MOE, and LWP were higher, while the growth rate and MFA were lower in Lagfors. Wood density and LWP decreased, while ring width increased (faster growth), after age 18 years in Övra. Similarly, such decreases in wood density and LWP, associated with faster growth, have previously been reported for white spruce (Park et al. 2012).

Genetic parameters

Heritability estimates of area-weighted densities (density, EWD, LWD, and TWD) obtained for the current lodgepole pine study were comparable with those of other coniferous species. Such estimates for MFA (0.30 in Övra, 0.33 in Lagfors) and MOE_S (0.30 in Övra, 0.13 in Lagfors) were lower than those reported in radiata pine (0.61 and 0.50; Wu et al. (2008)) but similar to those reported in Scots pine (0.26 and 0.37; Hong et al. (2014)) and Norway spruce (0.15 and 0.33; Chen et al. (2015)). Area-weighted densities and ring width proportions (EWP, TWP, and LWP) had greater heritability estimates than those of MFA and stiffness (MOE_S and MOE_{tof}). This observation agree with estimates in other conifers (Baltunis et al. 2007; Chen et al. 2014; Hong et al. 2014). In general, standard errors of heritability estimates in this study were high, particularly for MOE_S and MFA measured with SilviScan. This might be due to compression wood, which affects heritability estimates for wood quality traits (Donaldson 2008). Additionally, fewer sampled trees (e.g., four trees) per family in the current study than most other studies (5–12 trees) using SilviScan, might have incurred high standard errors. For future investigations, selection of more than four trees per family is desirable.

Unfavorable genetic correlations between wood density and growth traits is often reported (Zobel and van Buijtenen 1989) and strong adverse genetic correlations are usually observed in conifers (Fries 2012; Rozenberg and Cahalan 1997). Wu et al. (2008) summarized radiata pine studies and observed an average negative genetic correlation of −0.48 between wood density and DBH. Negative genetic correlations between growth and wood density were also observed in Scots pine (−0.48) and Norway spruce (−0.60) (Hong et al. 2014; Chen et al. 2014). These studies also reported stronger negative genetic correlations between growth and stiffness. Similarly, genetic correlation of DBH with density (−0.24 in Övra and −0.31 in Lagfors), MOE_S (−0.51 in Övra and −0.80 in Lagfors), and MOE_{tof} (−0.35 in Övra and −0.14 in Lagfors) were unfavorable in this study. Therefore, tree breeders must consider this unfavorable genetic correlation in designing breeding programs. There are several methods reported in dealing with such adverse correlations, including estimating economic weights to improve growth and

Fig. 3. Age–age genetic correlations between earlier ages and the reference age of 26 years in wood properties for (*a*) cumulative ring width, (*b*) wood density, (*c*) MFA, and (*d*) MOE from cambial age 1 to age 26 at breast height, based on area-weighted values, for the two trials of lodgepole pine. [Colour online.]



wood quality traits simultaneously (Ivković et al. 2010), designing effective breeding strategies (Wu and Sanchez 2011; Yanchuk and Sanchez 2011; Hallingbäck et al. 2014), and using index selection such as restricted index (Chen et al. 2016).

In conifers, MFA varies significantly from pith to bark (Donaldson 2008), and such great within-tree variation hinders accurate measurement of MFA properties in trees (Brändström 2002); therefore, MFA of large numbers of tracheids are needed to be measured to obtain accurate MFA values in trees (Gräns et al. 2009). Additionally, the relationship between MFA and density is a controversial subject in the literature as it varies within and among species (Baltunis et al. 2007; Donaldson 2008). Such correlation was negative in Scots pine, radiata pine, and Norway spruce (Chen et al. 2014; Dungey et al. 2006; Hong et al. 2014), whereas Bergander et al. (2002) found no correlation between MFA and density in Norway spruce (Bergander et al. 2002). In this study, we found a low to moderate positive correlation between MFA and density associated with high standard errors. In white spruce, Lenz et al. (2011) also found a high to moderate correlation between density and MFA in rings near the pith and hypothesized that both traits could be genetically linked during formation of juvenile wood (Lenz et al. 2011). Strong negative (but favorable) correlation between MOE and MFA obtained in this study agrees well with findings in other conifers (Baltunis et al. 2007; Cave and Walker 1994; Chen et al. 2014) and indicates that selection for reduced MFA would produce gains in MOE and overall improvement of lodgepole pine stiffness.

Early selection efficiency

There is usually a transition from juvenile to mature wood phases for wood properties from pith to bark in pine species (Burdon et al. 2004; Loo et al. 1985). Juvenile wood generally has lower quality when compared with mature wood (Wang and Stewart 2012). Therefore, improvement of juvenile wood is highly important. Besides the juvenile wood, the whole-core wood can be improved through early selection if there is a high age–age genetic correlation. Age–age genetic correlations and efficiency of early age selection of lodgepole pine were examined. Age–age genetic correlations from early ages to the reference age of 26 years for wood density, MFA, and MOE were very high in this study, which implies that early selection for wood quality traits is highly efficient if heritability at early ages was comparable or higher than at later ages. In this study, MFA had the most potential for early age selection, as efficiency reached unity at ring 4 at both trials. Similarly, in white spruce and Norway spruce, MFA was the most potential trait for selection as early as ring 4 (Chen et al. 2014; Lenz et al. 2011). Several investigations in conifers such as radiata pine (Li and Wu 2005; Wu et al. 2007), Scots pine (Hong et al. 2015), white spruce (Lenz et al. 2011), and Norway spruce (Chen et al. 2014) revealed that early selection is more efficient in wood quality traits than in growth traits due to the higher heritability and higher age–age correlation of wood quality traits compared with growth traits. Results of this study showed that early selection at age 3 for wood density and MFA and at age 10 for MOE was as efficient as the reference age in Övra. Similarly, early selection at age 3 for MFA and MOE and at age 9 for wood density was as efficient as the reference age 26 in Lagfors. Lower efficiencies of

Fig. 4. Efficiencies of early selection between earlier ages and the reference age of 26 years in wood properties for (*a*) cumulative ring width, (*b*) wood density, (*c*) MFA, and (*d*) MOE from cambial age 1 to age 26 at breast height, based on area-weighted values, for the two trials of lodgepole pine. [Colour online.]

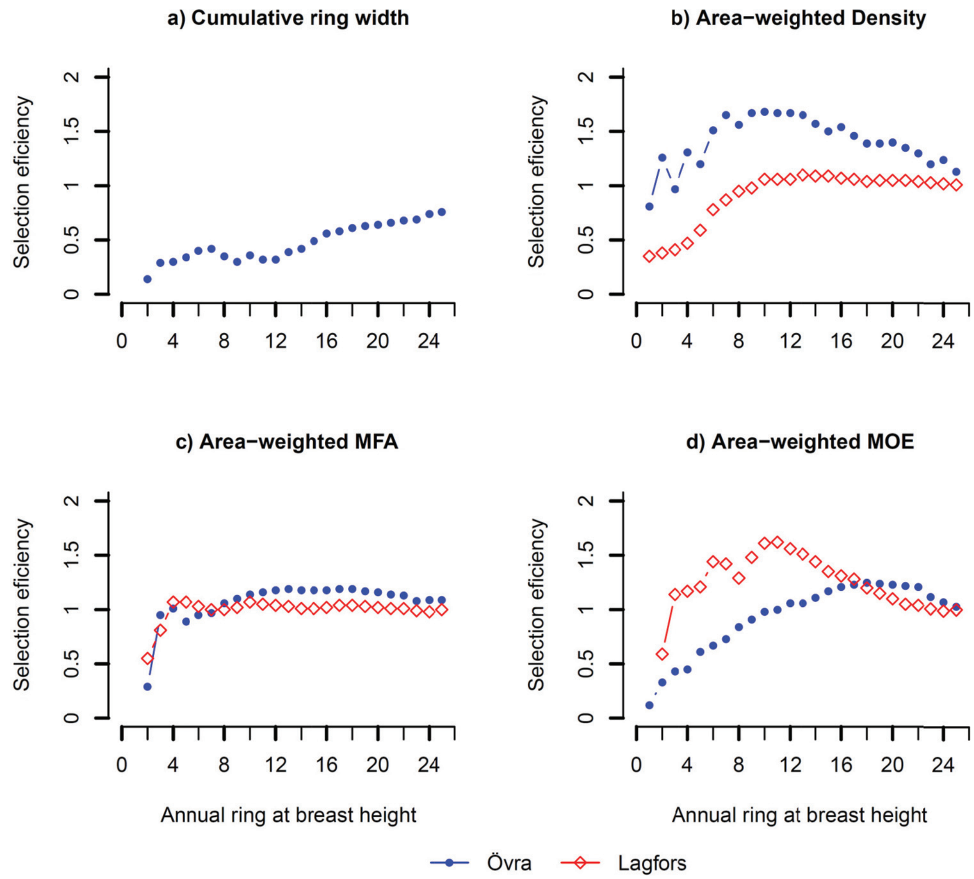


Table 4. Genetic gains and correlated genetic responses for DBH, MOE_S, and MOE_{tof} at Övra and Lagfors.

Selection trait	Response (%) DBH	MOE_S	MOE_{tof}
DBH	**7.9**	–5.5	–2.3
MFA	4.5	–9.6	–8.0
MOE_S	–6.5	**13.0**	11.4
MOE_{tof}	–3.0	12.5	**12.7**

Note: Values in bold indicate normal, genetic response. DBH, diameter at breast height; MFA, microfibril angle; MOE_S, modulus of elasticity from SilviScan; MOE_{tof}, modulus of elasticity from acoustic velocity.

early age selection for MOE in Övra and for wood density in Lagfors are due to lower heritability and lower age–age correlation found in these traits.

Genetic gains

As the breeding program of lodgepole pine progresses, it becomes more vital to incorporate solid-wood properties, i.e., stiffness, as main selection criteria in advanced generations of Swedish lodgepole pine. The expected genetic gains obtained for stiffness, if selection was made based only on MOE_S and MOE_{tof}, were about 13.0%. However, due to the unfavorable genetic correlation between growth and stiffness, selection for 1% increase in DBH would result in 5.5% and 2.3% decreases in MOE_S and MOE_{tof}, respectively.

Conclusion

1. Wood density, MOE_S, and LWP increased from the pith, while MFA and ring width were high around the pith then gradually decreased and stabilized towards the bark. In general, radial age trends were similar at both trials, though stiffness and LWP were greater and ring width was less in Lagfors, after the 18 years of cambial age.
2. Inheritance pattern of wood density was very similar at both trials and heritability reached the maximum value of about 0.6 in Övra and 0.9 in Lagfors between ages 6 to 14 years of cambial age. Ring width, MOE_S, and MFA were more heritable in Lagfors around the pith. However, heritability estimates of ring width reached zero near the bark in Lagfors, while it reached around 0.2 in Övra. Heritability estimate of MOE_S and MFA reached around 0.2 and 0.3, respectively, at both trials.
3. Genetic correlations between the early age and the reference age of 26 years were very high (~0.8 after age 5), suggesting that early selection is efficient at age 4 for MFA and between ages 5 to 8 years for density and MOE_S.
4. Adverse genetic correlations between growth and wood quality traits were found in this study. Breeding for 1% increase in growth (diameter) would result in decreases of 5.5% and 2.3% in lodgepole pine stiffness (MOE_S and MOE_{tof}, respectively). Therefore, index selection with appropriate economical weights for growth and stiffness is highly recommended for breeding selection.

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