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ORIGINAL PAPER

Genetic parameters, genetic gain and correlated responses in growth, fibre dimensions and wood density in a Scots pine breeding population

Anders Fries

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Abstract
• ***Context*** The multi-trait analyses of a progeny trial presented here will provide advice for including wood and fibre traits in the current Scots pine (*Pinus sylvestris* L.) breeding programs.
• ***Aims*** Fibre length and fibre width were analysed together with area-weighted earlywood and latewood densities and growth traits in a Scots pine full-sib progeny trial to estimate heritabilities, genetic correlations and genetic gain.
• ***Methods*** Wood density was analysed by X-ray diffraction of increment cores and fibre dimensions with a Kajaani FiberLab analyser. Genetic parameters were estimated using the ASReml statistical software.
• ***Results*** Heritabilities for fibre width, fibre length, height growth and earlywood, latewood and whole-ring density were 0.22 to 0.49. Fibre width exhibited positive genetic correlation with height growth (r_A=0.24) and wood density (r_A=0.096 to 0.32). Fibre length exhibited negative correlations with height and stem diameter (r_A=−0.27 and r_A=−0.59, respectively) but positive with wood densities (r_A=0.26 to 0.37). Growth traits and wood densities were negatively genetically correlated.
• ***Conclusions*** Selecting the trees in the top 10 % for height will give minor increase in fibre width (+1 %), and decrease in relative fibre length (−0.84 %) and area-weighted earlywood, latewood and whole-ring densities (−1 % to 1.9 %) indicating limited scope for combining improvements in wood and fibre traits with increased growth through breeding.

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1 Introduction

Wood products from forestry are very important raw materials with many uses. Three of the most important products in this category are sawn timber, pulp for paper production and bioenergy. Forestry is particularly important in Sweden, where it is one of the major national industries. The major products of the Swedish forestry industry are sawn timber and pulp, primarily from Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.); 16.1 million m^3 of sawn timber and 11.5 million tons of pulp were produced in 2010 (Skogsstyrelsen 2011, p. 219, 221 and 224). Around 22 % of the pulp is used to produce newsprint and 50 % is turned into paperboard, which necessitates the use of high-strength pulp and paper. The quality of the sawn timber and pulp is strongly dependent on the characteristics of the various components of the wood (see e.g. Watson and Bradley (2009) and Finell (2003)). In particular, the properties of the fibres have a profound influence on the properties of the wood and the pulp and paper produced from it.

There are a number of descriptions for the structure of the wood. In the traditional description, the first growth rings surrounding the pith are regarded as juvenile wood, which is in turn surrounded by a transition zone and then by mature wood (Zobel and Jett 1995). Furthermore, each annual ring includes both earlywood and latewood, with earlywood being formed during active growth and latewood being formed at the end of the growing season. In a thorough review of the different wood types in radiata pine (*Pinus radiata*), Cown (1992) stated that compared to the mature wood, juvenile wood (also known as corewood) has shorter fibres with thinner cell walls,

a higher spiral grain, a lower proportion of latewood (and thus a lower density), more dry knots and a lower cellulose content. Both the mature wood and the earlywood primarily contain long and slender fibres with a low weight per unit length, i.e. low coarseness. Furthermore, the pulp produced from wood with long and slender fibres has a high reinforcement strength (Hannrup et al. 2004) and is therefore suitable for kraft paper (Watson and Bradley 2009). Conversely, the shorter fibres and thinner cell walls of the central juvenile wood means it produces kraft pulp and kraft paper with poorer quality (Watson and Bradley 2009).

Earlywood and latewood differ in terms of their fibre characteristics. Earlywood fibres are predominantly long and slender, with a comparatively low density. In contrast, the cells of latewood fibres are short and thick-walled (Zobel and Jett 1995, p. 82), and thus produce less strong pulp and paper (Watson and Bradley 2009). However, the short fibres make latewood pulp suitable for producing fine paper (Finell 2003). Notably, woods with long and slender fibres generally have stronger bonding between fibres and a greater number of fibres per ton of pulp, which is advantageous for most types of papers. On the other hand, the thick-walled fibres common in latewood give it a relatively high density, and one would thus expect fibre length to correlate negatively with wood density and fibre width.

When deciding what kind of paper should be produced from a given batch of wood, the differences in properties of the different wood types and fibres make it important to know the different proportions of wood in the batch. That is, one must determine whether it consists primarily of juvenile or mature wood and whether it is mostly earlywood or latewood (Arlinger and Wilhelmsson 1999; Watson and Bradley 2009). Moreover, since woods with different types of fibres should be treated differently in the pulping process, a well-defined and highly uniform wood product facilitates optimization of the pulping process (Watson and Bradley 2009).

In Scots pine breeding in Sweden, volume production together with good adaptation to the current and future predicted conditions has been the focus. However, in recent years there has been a growing level of interest in the wood quality traits discussed above. When breeding for volume growth, one of the key goals is to make effective use of the growing season and to have the tree go through the growth cessation process rapidly to avoid climate damage in the autumn. Achieving strong late summer growth while allowing for adaptation to the climate is likely to be challenging, and will affect volume production as well as the ratio of earlywood to latewood and thus the wood density and fibre dimensions (Ståhl 1988). Hannrup and Ekberg (1998) demonstrated that there is a strong genetic correlation (r_A=0.92) and a relatively strong phenotypic correlation (r_P=0.36) between fibre length in juvenile wood (the fourth annual ring from pith at breast height) and transition or early mature wood (the 24th annual ring), which should increase the scope for early selection for fibre length, as also indicated by Fries et al. (2003). Similar results were reported for earlywood and latewood densities by Fries and Ericsson (2009). However, there is a general lack of studies on the genetic relationship between wood density and fibre dimensions in Scots pine and other pines, with phenotypic correlations more often being identified, e.g. by Gort et al. (2009) and Mansfield et al. (2009).

It is evident that selection for improvement of growth capacity, wood density and fibre properties simultaneously would be difficult. However, since all of them are important, it would as a bare minimum be necessary to control the impact on wood density and fibre characteristics when selecting for height growth. The study described herein was therefore conducted to evaluate genetic parameters relating to fibre dimensions, wood density and growth, and to evaluate the genetic relationships between these traits in Scots pine trees that are representative of the breeding population in Northern Sweden. The results obtained should be useful in predicting the response of these traits under selection for height and the genetic gains achievable when selecting for the traits themselves.

2 Material and methods

2.1 Test material and base data

The analysed material originated from increment cores (diameter 5 mm) collected in September 2001 in a full-sib progeny trial of Scots pine in Northern Sweden (S23F711261 Grundtjärn, at 63°33′ N, 17°25′ E at 320 m elevation). The trial was established by Skogforsk on non-sloping sandy moraine with an average site index for the locality, i.e. ca.T20 (that is to say, the projected dominant height after 100 years is approximately 20 m, corresponding to a site productivity of about 3 stem cubic metres including bark per hectare per year) (Hägglund and Lundmark 1982). It was planted in September 1971 in single tree plots with 179 full-sib families from 40 genetically selected parents and five reference seed lots. All controlled crosses except three were made in the same seed orchard, Nedansjö, at latitude 62°20′ N, 16°45′ E and an elevation of 60 m. The plus tree parents originated from the area between latitude 63° N and 64° N. Between one and nine trees from every family except one of the total 179 full-sib families were included in the analyses. The sampled area was subdivided into seven almost square, equal-sized blocks. Trees from five blocks were analysed in this work: 170–240 from each of the first four blocks and 77 from the fifth.

The wood samples were collected after 31 growing seasons from seed. To avoid causing excessive damage to the progeny trial, increment cores were generally not taken to the pith. On the basis of a limited number that were taken to the pith, along with data for previous increment cores taken to the pith in a parallel and even-aged field trial in the same test series (Ericsson and Fries 2004), it was estimated that the ten annual rings analysed were laid down when the tree was between 12 and 21 years old in breast height. Fibre dimensions were analysed for two annual rings outside the part used wood density analyses, i.e. ring numbers 22 and 23 from the pith. The rings were not analysed separately as they were so thin, and earlywood and latewood were analysed together.

The earlywood and latewood density data for individual trees that were used in the present study were those obtained in the analyses by Fries and Ericsson (2006; 2009). The used data for density and growth in this work differ, however, from those reported in Fries and Ericsson (2006; 2009) because in this case, only trees whose wood was analysed for fibre dimension were considered. This should allow for accurate comparisons of different traits and give more reliable correlations between fibre size and density and growth figures. The densities were analysed with X-ray diffraction technique with the Itrax Density Scanner (Cox Analytical Systems, Gothenburg, http://www.coxsys.se [Jan 2012]) (Fries and Ericsson 2006, 2009). In the analyses, the border between the earlywood and latewood was automatically set at 50 % of the difference between minimum and maximum density for the ring, while the borders between annual rings were defined manually after visual examination of X-ray images. Manual adjustments were also made to account for leaning borders between the earlywood and latewood and between annual rings of the increment cores. In the visual examination of the increment cores, miscoloured or damaged annual rings, often due to compression wood, and rings with cracks were excluded leaving 73 % of the annual rings as useable. Tree heights and stem diameters were measured when the wood samples were collected in 2001. In total, 897 trees were analysed.

2.2 Area-weighted density data

To analyse the area-weighted wood density, the area of each annual ring section (both earlywood and latewood) was weighted with the corresponding wood density. The principle for calculating the annual ring section area was to estimate the difference between the area of the cross-section of the stem from the pith to and including the target ring section minus the cross-section area from the pith to but excluding the target ring section. Annual ring widths inside ring 12 were lacking, and instead the radius of the circular section inside annual ring 12 (r_C) was calculated. For this were total stem diameter including bark (d01) and the annual ring widths from ring 12 to the bark used. Since the bark was included in the stem diameter was the bark thickness also needed in the calculations. The equations used were thus the following:

$$r_C = \mathrm{d01}/2 - \mathrm{Bark\text{-}th}/2 - \left(\left(\sum \mathrm{EW}_{12\to 21} + \sum \mathrm{LW}_{12\to 21}\right) - 2 \times \mathrm{EW21} - 2 \times \mathrm{LW21}\right)[\mathrm{mm}], \quad (1)$$

where Bark-th is the total bark thickness at breast height (i.e. both sides) and EW and LW are the widths of the earlywood and latewood sections in each annual ring. The subtraction of 2×EW21 and 2×LW21 in Eq. 1 is intended to reduce the total diameter by the width of the annual rings used for fibre dimension measurements (rings 22 and 23), which were assumed to have the same width as annual ring 21. Bark thickness (Bark-th) was estimated using the equation for Scots pine in Central North Sweden (Norrlands Skogsvårdsförbund 1962):

$$\mathrm{Bark\text{-}th} = \mathrm{d01} \times 0.1 + 2\,[\mathrm{mm}]. \quad (2)$$

To estimate the total area-weighted wood density of the ten annual rings, the density of each annual ring section was then weighted against its area using the expression developed by Hylen (1997) for the area-weighted earlywood density (AwED):

$$\mathrm{AwED} = \sum_{i=12}^{21} \mathrm{ED}_i \times \mathrm{EwArea}_i \Big/ \sum_{i=12}^{21} \mathrm{EwArea}_i, \quad (3)$$

where ED_i is the earlywood density of ring i and EwArea_i is the earlywood ring area for ring i. The corresponding equations for area-weighted latewood density (AwLD) and area-weighted total density (AwDtot) were used. A circular stem and circular annual rings are assumed and the equation of the area of a circle was the used.

2.3 Fibre dimension data

Annual rings 22–23 were macerated according to the protocol of Ericsson and Fries (2004) and the fibre suspensions were analysed using a Kajaani FiberLab 3.0 analyzer (Metso Automation Inc., Kajaani, Finland). In each analysis, 3,000–4,000 fibres were processed at a speed of 15–20 fibres per second and classified optically in 1 μm wide sections using photocells. Approximately 1/3 of the fibres were also classified lengthwise in 0.05-mm long sections. The estimated lengths of the wood fibres were considerably lower than the real lengths (1.6 mm, compared to the more typical values of ca. 3 mm for annual rings 20–25; Hannrup and Ekberg 1998) because the wood samples were obtained from 5-

mm increment cores, with the effect that the wood fibres were frequently cut. To account for this, the relative fibre length (RelLTH) was considered rather than the absolute length. For each analysis, the length-square-weighted mean length was calculated using the equation:

$$\text{RelLTH} = \sum n \times l_i^3 \Big/ \sum n \times l_i^2, \tag{4}$$

where n is the number of fibres in each 0.05-mm length section and l_i is the mid-section length for section i. Length-square-weighted mean lengths were used instead of length-weighted means or arithmetic means because the length-square-weighting substantially eliminates the influence on the mean of a large number of small fragments of broken fibres and other fragments which not are distinguished from intact fibres by the analyzer (Çöpür and Makkonen 2007) (Fig. 1). This weighting is, however, sensitive to erroneously long fibres such as fibres that are attached to one another as they pass through the measurement device. Consequently, data for fibres longer than 3.5 mm were excluded in subsequent calculations. In addition, a minimum length of 0.5 mm was stipulated (see Fig. 1). Since heritabilities are quotients of variances, relative values for fibre length, here RelLTH, can be used to obtain relevant estimates of heritability for fibre length, as demonstrated by Fries et al. (2003). Fibre lengths in a reference material consisting of undamaged wood samples were shown to correlate very strongly with relative fibre lengths from 5-mm increment cores (r_P= 0.8 for annual rings 13 to 16 from pith; Fries et al. 2003). Moreover, the variation in fibre lengths was similar for the two sample types. With these upper and lower limits useful data for estimating relevant genetic parameters were obtained. Arithmetic mean fibre widths were used because this measure was assumed to be insensitive to fragmentation. To exclude fragments and fibres that had become stuck together side by side, lower and upper width limits of 14.5 and 54.5 μm, respectively, were imposed. RelLTH was assumed to follow normal distribution (cf. Mörling et al. 2003), and normal distribution was assumed also for WTH.

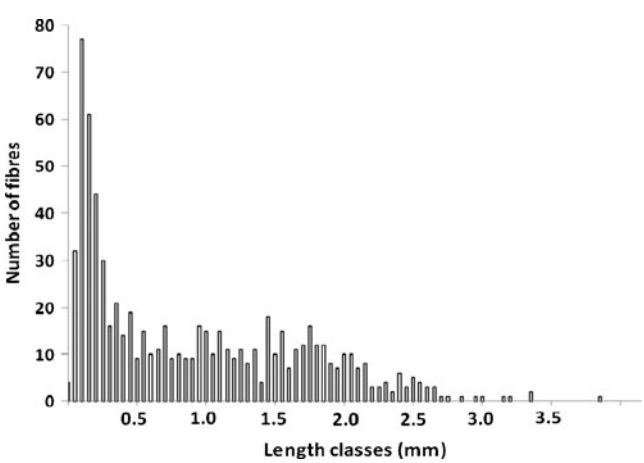

Fig. 1 Illustration of output data from the Kajaani FiberLab analyzer before filtering. The *bars* show the distribution of fibres in the different 0.05-mm length classes

2.4 Genetic model

The analyses were conducted using the REML method of the ASReml 2.0 statistical software package (Gilmour et al. 2006). The complete genetic model used has been described elsewhere (Fries and Ericsson 2006). The calculated heritabilities and genetic coefficients of variation obtained from the REML analyses were considered significant if the quotient of the variance component from which they were estimated and its standard error was ≥2. This is approximately equivalent to a significance level of $p \leq 0.05$, which is the significance level used in the text.

In brief, the genetic model was based on the equation $P=A+E$, i.e. a lack of significant specific full-sib family and reciprocal effects were assumed. Here, P is the phenotypic value, A the additive genetic effect and E the independent environmental effect including the genetic residual. The corresponding variances were assumed to be

$$\sigma_P^2 = \sigma_A^2 + \sigma_E^2 \tag{5}$$

The statistical model used for individual tree-based multi-trait analyses of the data set was constructed with one term for fixed effects (including only block effects) and another for random effects. The random term, which is connected to the genetic model, was constructed to incorporate genetic effects and linked to the parents of the full-sib families through a design matrix and a relationship matrix that was derived from the trees' pedigrees. This individual tree model separates the additive genetic and remaining (residual≈environmental) effects. Similarly, the covariances in the multiple-trait analyses were computed as $\sigma_{P_{ij}} = \sigma_{A_{ij}} + \sigma_{E_{ij}}$ for traits i and j. A variance (σ_A^2) for a trait i could equivalently be written as $\sigma_{A_i}^2 = \sigma_{A_{ii}}$ in multiple-trait notation. The narrow-sense heritability, $\widehat{h}_i^2$ was defined as the ratio of the additive genetic variance to total phenotypic variance and was calculated as described by Falconer and Mackay (1996, p. 169):

$$\widehat{h}_i^2 = 4\widehat{\sigma}_{\text{par}}^2 \Big/ \left(2\widehat{\sigma}_{\text{par}}^2 + \widehat{\sigma}_{\text{res}}^2\right), \tag{6}$$

where $\widehat{\sigma}_{\text{par}}^2$ is the variance for a mother or father (a lack of reciprocal effects was assumed) and $\widehat{\sigma}_{\text{res}}^2$ is the residual variance.

The additive genetic correlation between trait i and j, $\widehat{r}_{A_{ij}}$, was estimated according to Falconer and Mackay (1996):

$$\widehat{r}_{A_{ij}} = \widehat{r}_{A_iA_j} = \frac{\widehat{\sigma}_{u_iu_j}}{\widehat{\sigma}_{u_i}\widehat{\sigma}_{u_j}}, \tag{7}$$

and the additive genetic coefficients of variation, CV_{A_i}, as:

$$\widehat{C}V_{A_i} = \widehat{\sigma}_{A_i}/\text{phenotypic mean, where } \widehat{\sigma}_{A_i} = \sqrt{\widehat{\sigma}^2_{\text{fam}}(i)}. \quad (8)$$

Approximate standard errors were obtained from the basic error variance estimates and first-order Taylor expansion.

Height growth is a major selection criterion in most breeding programs, including the Swedish Scots pine program. The expected genetic responses in different target traits under backward selection for height were therefore estimated. The estimates were based on the following equation:

$$\Delta G_{\text{h01},i} = i \times r_{\text{TI}}(\text{h01}) \times r_A(\text{h01}, i) \times \sigma_A(i), \quad (9)$$

where $\Delta G_{\text{h01},i}$ is the genetic response in trait i when selecting for height, i is the selection intensity, r_{TI}(h01) is the breeding value prediction accuracy for height, r_A(h01,i) is the genetic correlation between height growth and the target trait in question, and σ_A (i) is the genetic standard deviation for the target trait (Hallingbäck 2010).

Breeding value accuracy, r_{TI}(h01), i.e. the correlation between the true and predicted breeding values for height, was estimated using the following equation:

$$r_{\text{TI}} = \frac{\sigma_I}{\sigma_A}, \quad (10)$$

where σ_I is the standard deviation of the predicted breeding values and σ_A is the genetic standard deviation for the selection trait, i.e. height (Hallingbäck 2010).

The genetic response expressed as percentage of the mean in direct selection for trait i was estimated as:

$$\Delta G_i = i \times \widehat{h}^2_i \times \sigma_P(i) \times \frac{100}{Mv_i}, \quad (11)$$

where Mv_i is the mean value of trait i (Falconer and Mackay 1996).

3 Results

3.1 Mean values, phenotypic and genetic variation and heritabilities

Mean values, genetic and phenotypic standard deviations, and coefficients of variations for growth, fibre dimensions and density data are given in Table 1. Genetic coefficients of variation varied between 2.0 % and 6.3 %, with the lowest coefficients for fibre dimensions. Phenotypic coefficients of variation were approximately twice as high as the corresponding genetic coefficients for all parameters other than stem diameter at breast height (d01) and relative fibre length (RelLTH), for which the coefficients were 3.3 times and 36 times the genetic coefficients, respectively.

Table 2 shows the heritabilities and genetic and phenotypic correlations along with the corresponding standard errors. The heritability for fibre width (WTH) was high (h^2=0.49) while it was lower for RelLTH (h^2=0.23) and height growth (h01) (h^2=0.30). The heritability for d01 was very low (h^2=0.094) and those for the area-weighted wood densities ranged from h^2=0.22 to h^2=0.34 with whole-ring wood density having the greatest value. The standard errors for the heritabilities ranged from 24 % to 43 % of the heritability values.

3.2 Genetic and phenotypic correlations between traits

The genetic correlation between h01 and d01 was reasonably strong but not significant, r_A=0.47 (Table 2). However, d01 correlated significantly with RelLTH (r_A=−0.59) and area-weighted whole-ring density (AwDtot; r_A=−0.58). Moreover, there were significant genetic correlations between the different area-weighted densities, with the weakest being that between AwED and AwLD (r_A=0.79). With the exception of d01 and RelLTH (see above), the genetic correlations between growth traits and fibre dimensions were weak. There was a non-significant positive genetic correlation between the fibre dimension traits WTH and RelLTH (r_A=0.35). Even though area-weighted densities were used, all of the studied wood density traits exhibited negative but generally non-significant genetic correlations with growth traits: from r_A=−0.14 to r_A=−0.22 with h01 and from r_A=−0.48 to r_A=−0.58 with d01. There were positive but non-significant genetic correlations between densities and fibre dimensions (r_A=0.10 to r_A=0.37).

The strongest phenotypic correlations observed were between h01 and d01 (r_P=0.65, $p \leq 0.05$) and between different measures of wood density (r_P=0.52 to r_P=0.92, $p \leq 0.05$). As was the case for genetic correlations the weakest phenotypic correlation for wood densities was between AwED and AwLD. All other significant phenotypic correlations were low (r_P=−0.21 to r_P=0.31) with negative correlations between d01 and density traits, positive between WTH and growth, and RelLTH and AwLD. h01 showed very low phenotypic correlations with density traits.

3.3 Genetic gain and correlated response

The genetic gain (ΔG) for within-trait selection was highest for h01 and WTH: ΔG_{h01}=+5.3 % and ΔG_{WTH}=+5.0 %, respectively, with selection of the 10 % best individuals (Table 3). The genetic gain for relative fibre length RelLTH was lower: ΔG_{RelLTH}=+1.7 % at a selection intensity of 10 %, partly as a result of low phenotypic variation. The responses for area-weighted densities (AwED, AwLD and AwDtot) were intermediate (ΔG_{WTH}=+3.2 % to 4.2 %) with the strongest being that for AwED. As expected, selection for one of the

Table 1 Mean values (*Mv*), genetic and phenotypic standard deviations (σ_A and σ_P, respectively) and genetic and phenotypic coefficients of variation in percent (CV_A (%) and CV_P (%), respectively)

	Mv	σ_A	CV_A(%)	σ_P	CV_p(%)
h01 (dm)[a]	112.3	6.195	5.52	11.23	10.00
d01 (mm)[a]	155.7	9.86	6.33	32.12	20.63
WTH (μm)	31.73	0.831	2.62	1.831	5.77
RelLTH (mm)	1.585	0.0325	2.05	1.183	74.64
AwED (g/cm^3)	0.357	0.0172	4.81	0.0341	9.55
AwLD (g/cm^3)	0.722	0.0349	4.83	0.0743	10.29
AwDtot (g/cm^3)	0.456	0.0246	5.38	0.0423	9.28

h01 height growth, *d01* stem diameter at breast height including bark, *WTH* fibre width, *RelLTH* relative fibre length, *AwED* area-weighted earlywood density, *AwLD* area-weighted latewood density, *AwDtot* area-weighted whole-ring density

[a] Growth data differ slightly from Fries and Ericsson (2006, 2009) since fewer trees are included here (see Section 2)

density traits generated a strong correlated response (CR) in other density traits, CR=+5.6 % to 7.4 %. Unsurprisingly, when selecting for height, the trait with the largest positive correlated response was stem diameter, with a correlated response of $CR_{h01,d01}$=+4.6 % (Table 3; Fig. 2). Although area-weighted densities were used, the correlated responses for the combination of area-weighted densities and d01 were negative (CR=−2.9 % to CR=−5.7 %). The correlated responses including h01 were lower (CR=−1.0 % to CR=−1.9 %). Selection for RelLTH would yield a clear negative correlated response in growth traits, CR=−2.4 % and CR=−6.0 % for h01 and d01, respectively, when selecting the top 10 %, whereas selection for WTH generally yielded only minor changes in growth traits (CR=−0.07 % to CR=+2.0 %). It seems that it would be possible to simultaneous select for increased fibre size and wood density: all correlated responses for these traits were positive, albeit not very large (CR=+0.4 % to CR=+2.7 %).

4 Discussion

4.1 Heritability

The heritability for height (h01) was h^2=0.30, which is comparable to or slightly higher than results obtained in

Table 2 Correlations of the relationship between the analysed traits (abbreviations, see Table 1)

		h01	d01	WTH	RelLTH	AwED	AwLD	AwDtot
				r_A				
h01		***0.305***	0.471	0.240	−0.268	−0.219	−0.139	−0.225
		0.084	0.189	0.185	0.203	0.202	0.211	0.195
d01		0.648[a]	***0.094***	−0.007	−0.587[a]	−0.484	−0.485	−0.579[a]
		0.021	***0.040***	0.238	0.222	0.219	0.227	0.196
WTH	r_P	0.237[a]	0.186[a]	***0.493***	0.350	0.117	0.316	0.096
		0.041	0.035	***0.117***	0.179	0.198	0.186	0.192
RelLTH		−0.003	0.032	0.313[a]	***0.227***	0.344	0.264	0.367
		0.038	0.035	0.036	***0.068***	0.198	0.211	0.189
AwED		−0.071	−0.164[a]	−0.046	0.053	***0.253***	0.787[a]	0.920[a]
		0.038	0.033	0.042	0.037	***0.073***	0.097	0.033
AwLD		0.068[a]	−0.111[a]	0.121[a]	0.035	0.524[a]	***0.221***	0.922[a]
		0.038	0.033	0.040	0.036	0.026	***0.067***	0.042
AwDtot		−0.020	−0.214[a]	−0.001	0.042	0.901[a]	0.922[a]	***0.337***
		0.041	0.033	0.044	0.039	0.007	0.042	***0.090***

Heritabilities (h^2) in italics along the diagonal, additive genetic correlations r_A above the diagonal, phenotypic correlations r_P below the diagonal. In small text below the standard errors (SE(h^2) (also in bold and italics), SE(r_A) and SE(r_P), respectively)

[a] The genetic variance component is more than 2.0 times the standard error approximating a significance of ca 95 % (see Section 2)

Table 3 Genetic gain and correlated genetic response

Response trait		h01	d01	WTH	RelLTH	AwED	AwLD	AwDtot
Selection criteria	h01	***5.34***	4.58	0.97	−0.84	−1.62	−1.03	−1.86
	d01	3.27	***3.41***	−0.02	−1.52	−2.93	−2.96	−3.93
	WTH	1.97	−0.07	***4.99***	1.06	0.83	2.26	0.77
	RelLTH	−2.38	−5.99	1.47	***1.72***	2.66	2.06	3.19
	AwED	−1.82	−4.60	0.46	1.06	***4.24***	5.72	7.45
	AwLD	−1.14	−4.53	1.22	0.80	5.58	***3.98***	7.33
	AwDtot	−1.93	−5.70	0.39	1.17	6.88	6.93	***3.19***

Genetic gain (ΔG) in percentage from within-trait selection (italics in the diagonal) and correlated genetic response (CR) in percentage in target traits (above and below diagonal). The percentages are based on selection of the 10 % best in the selection criteria trait. For the abbreviations, see Table 1

previous studies on the same full-sib families (Ericsson and Fries 2004; Fries and Ericsson 2006, 2009) and for Scots pine in general (Kroon et al. 2008, 2011) (Tables 2 and 4). That for breast height diameter (d01) was lower (h^2=0.09) with the relative standard error in relation to the heritability value being higher than for the other traits considered. Breast height diameter has previously been reported to have an exceptionally low heritability (Atwood et al. 2002) (Table 4), probably because the study in question focused on 13 progeny trials spread over a wide geographical range, generating a large genotype×environment interaction. Similar heritabilities were estimated in large-scale evaluations of Swedish progeny trials with Scots pine (h^2=0.05 to 0.11; Kroon et al. 2008). On the other hand, based on two progeny trials with maritime pine (*Pinus pinaster*) Lepoittevin et al. (2011) reported h^2=0.32 for breast height diameter. The heritability of the stem diameter is known to be rather variable due to differences in stand density as a result of different mortality,

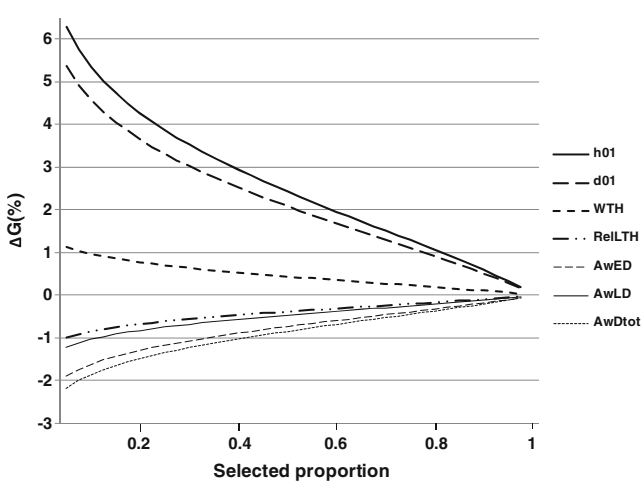

Fig. 2 Expected genetic responses in h01, d01, WTH, RelLTH, AwED and AwLD and AwDtot when selecting for height growth at different proportions. Abbreviations according to text

variation in tree size etc., which can give a relatively high environmental variance.

The heritability for fibre width (WTH) was unusually high in the present work while the heritability for height (h01) seems to be comparable to or higher than other studies (Tables 2 and 4). For fibre length (RelLTH), the heritabilities were in accordance with heritabilities from similar studies. It was however lower than that obtained in a field trial that was conducted in parallel (Ericsson and Fries 2004) which involved a larger sample size, but greater than that reported for fibre length in the latewood sections of the first ten annual rings of loblolly pine (*Pinus taeda*) by Loo et al. (1984): h^2_i=0.23, compared to h^2=0.30 and h^2_i=0.00 to 0.15, respectively. Conversely, in a review on radiata pine Wu et al. (2008) reported a number of comparatively high heritabilities for fibre length, with the average value from 14 different studies being h^2=0.54. The heritabilities obtained in this work are also lower than those reported for Scots pine by Hannrup and Ekberg (1998) and Hannrup et al. (2000): h^2=0.31 for annual ring 4 from pith and h^2=0.48 for annual ring 24 (in the present study, relative fibre lengths for rings 22 and 23 only were analysed). However, the results of Hannrup et al. (2000) are not fully comparable because their values and heritabilities were for the length of latewood fibres only and if they are more resistant to breakage than earlywood fibres, as claimed by Huang et al. (2008), the length estimates for the latewood fibres may be more precise leading to higher heritability estimates. A general recommendation due to the differences in fibre characteristics between earlywood and latewood is to analyse the wood types separately if they can be separated with high precision. It is furthermore probable that noise in the data due to fibre fragments and wood debris would have been minimized by using the image analyzer, giving a smaller residual variance and higher values for the genetic parameters, as also reported by Hannrup and Ekberg (1998) and Hannrup et

Table 4 Overview over heritabilities for growth traits, wood densities and fibre dimensions in studies of Scots pine and other pines

Species	Trait (age)					Reference	Density estimate
	Height	Stem diameter	Fibre width	Fibre length	Wood density		
P. sylvestris	0.30 (31)	0.09 (31)	0.49 (22–23)	0.23 (22–23)	0.22/0.25/0.34[a] (12–21)	Present study	Weighted
P. sylvestris	0.29 to 0.40 (31)	0.10 to 0.13 (31)	–	–	0.25/0.22[b] (12–21)	Fries and Ericsson (2006, 2009)	Un-weighted
P. sylvestris	0.23 (5–20)[c]	–	–	–	–	Kroon et al. (2011)	–
P. sylvestris	0.16 to 0.19 (30)[d]	0.05 to 0.11 (30)[d]	–	–	–	Kroon et al. (2008)	–
P. sylvestris	0.28 (25)	0.17 (25)	0.31 (14–22)	0.30 (14–22)	–	Ericsson and Fries (2004)	Un-weighted
P. sylvestris	0.24 (11–24)	0.14 (11–24)	–	–	0.28 (24)[e]	Haapanen et al. (1997)	Pilodyn
P. sylvestris	–	–	–	0.31/0.48 (4/24)	0.36 to 0.50 (1–26)[f]	Hannrup and Ekberg (1998)	Un-weighted and weighted
P. sylvestris	0.29 (13)	0.18/0.27 (13/33)	–	See: Hannrup and Ekberg (1998)	See: Hannrup and Ekberg (1998)	Hannrup et al. (2000)	Do
P. pinaster	0.46 (14)	–	0.18 (≤14)	0.19 (≤14)	0.29	Pot et al. (2002)	Un-weighted
P. taeda	–	–	–	0.15 (8)	–	Sykes et al. (2006)	–
P. taeda				0 to 0.15 (0–22, decreasing by age)[g]		Loo et al. (1984)	Un-weighted
P. taeda	0.07 to 0.09 (12–18)[h]	–	–	0.31/0.15/0.33[i] (8)		Atwood et al. (2002)	Un-weighted
P. radiata	–	–	0.54	–	0.3 to 1.0 (1–26 to 1–20)	Wu et al. (2008)[j]	Un-weighted and weighted

Within parenthesis are the ages for the estimates given (for fibre traits and wood densities, annual rings from pith)

[a] Area-weighted wood densities for earlywood, latewood and the whole ring, respectively. Estimates based on all 10 years

[b] Un-weighted whole ring, earlywood and latewood density, respectively. Heritabilities based on each annual ring separately: h^2 =0.08 to 0.27

[c] Estimate based on a numerous progeny tests with ages between 5 and 20 years

[d] Evaluated in ten progeny tests with totally more than 50,000 trees

[e] Density estimate as pilodyn value and thus only wood density for the outermost annual rings

[f] Fibre lengths estimated for the latewood section. Different age intervals and both un-weighted and area-weighted wood densities

[g] Fibre lengths estimated for the latewood section. Family heritability also decreasing; $h_{fam}{}^2$ =0.32 to 0

[h] This heritability interval is given for both height and stem diameter, and also juvenile, mature and total volume

[i] For juvenile, mature and total wood density, respectively

[j] Literature review where studies including different age intervals are covered

al. (2000). The high phenotypic coefficients of variation for RelLTH (CV_P=75 %; Table 1) indicate that the analytical method used in this work, i.e. automated optical registration of macerated fibre solutions, has limitations when applied to samples from thin increment cores. The low genetic coefficients of variation for RelLTH and WTH (which CV_A values of 2.12 % and 2.62 %, respectively; Table 1), it also indicate limited potential for genetic gain when based on present data. The variation in heritabilities for fibre dimensions demonstrates that this parameter depends on the test material, the environmental conditions during the test, and the techniques used in testing. This point is illustrated by the wide range of estimated heritabilities in different studies.

The area-weighted wood densities (AwED, AwLD and AwDtot) had heritabilities in the interval h^2=0.22 to 0.34 with the highest for AwDtot (Table 2). The standard errors in relation to the heritabilities were similar in each case, ranging from 27 % to 30 %. These heritabilities were based on the whole increment core section (annual rings 12–21). As a comparison the heritabilities for the un-weighted earlywood and latewood densities for individual annual rings were lower in the present material (h^2=0.08 to 0.27 for ED and h^2=0.1 to 0.24 for LD), with similar or slightly greater relative standard errors (Fries and Ericsson 2009). These heritabilities are similar to those reported by Atwood et al. (2002) for loblolly pine, slightly lower than those reported by Hannrup and Ekberg (1998) and Hannrup et al. (2000) for Scots pine, and considerably lower than those listed for radiata pine (Wu et al. 2008) (Table 4). In particular, the reported heritabilities for radiata pine were considerably greater than those observed in this work: the average heritability for earlywood and latewood densities combined was ca. 0.6. It is notable that in the present study, the heritability for AwDtot was considerably greater than that for the earlywood or the latewood individually although AwDtot is based on a mix of those two wood types. This could be due to the difficulty of accurately defining the boundary between earlywood and latewood when adjusting the borders between wood types and annual rings during the examination of the X-ray image. Since the densities of earlywood and latewood differ substantially, errors in the adjustment of these boundaries would significantly affect the results obtained. It might thus be better to avoid distinguishing between earlywood and latewood in wood density analyses or, if possible, exclude the transition zone between earlywood and latewood before analysis. Furthermore, a comparison of our previous results (Fries and Ericsson 2009) with those obtained in this work suggests that heritabilities based on area-weighted wood densities of whole increment cores are generally higher than those based on individual annual rings, as also noted by Wu et al. (2008).

4.2 Genetic correlations

The genetic correlations between height growth, which is a prioritized selection criterion, and fibre dimensions were divergent: that with fibre width (WTH) was positive (r_A=0.24) while that with relative fibre width (RelLTH) was negative (r_A=−0.27; Table 2). However, these correlations were non-significant and had standard errors that were comparable in magnitude to the correlations themselves. Moreover, if real, both of these correlations would be unfavourable when breeding wood suitable for kraft paper production, where long and slender fibres are desired (Hannrup et al. 2004). Similar relationships were obtained by Ericsson and Fries (2004); r_A=0.56 for fibre width and r_A=−0.12 for fibre length (in both cases, the standard errors were also of similar in size). Fibre measurements were in both of these studies conducted using an optical Kajaani FiberLab analyzer. In contrast to these results, Hannrup et al. (2004) observed a strong positive genetic correlation between height growth and fibre length (r_A=0.59) when using the same technique in studies on Norway spruce. Similarly, Pot et al. (2002) reported a positive and significant genetic correlation between tree height and arithmetic fibre length (r_A=0.80) but a negligible correlation with fibre width when using a similar instrument on maritime pine. Furthermore, the genetic correlation between fibre length and fibre width was positive (r_A=0.56, $p \leq 0.05$) which is in accordance with the result reported here (r_A=0.35, however not significant; Table 2). Zubizarreta Gerendiain et al. (2008) observed phenotypic correlations in a clonal material of Norway spruce (r_P[stem volume−fibre length]=0.23 and r_P[fibre width−fibre length]=0.64). With a microscope-connected image analyzer, Hannrup et al. (2000) observed a strong positive genetic correlation between height and fibre length with a much lower standard error (r_A=0.52, SE=0.16). Ivkovich et al. (2002a) used an image analyzer in a similar study of white spruce (*Picea glauca* Moench.) and Engelmann spruce (*Picea engelmannia* Parry ex Engelm.) and likewise reported a strong positive genetic correlation between ring width and fibre length (r_A=0.83). The instrument with the highest precision, Silviscan3, separates in addition tangential and radial fibre diameter and it was used in analyses of white spruce by Lenz et al. (2010). They reported positive genetic correlations between tree height and radial fibre width: r_A=0.52 and r_A=0.65 for earlywood and latewood, respectively, but negligible for tangential fibre diameter in the earlywood, r_A=−0.01 (not measured in the latewood). The different correlations for tangential and radial fibre diameters indicate that it can be meaningful to analyse these fibre diameters separately. The general trend seems therefore to be that height is positively genetically correlated with fibre length and fibre width. There are however exceptions which probably can be a result of the use of different techniques.

Both WTH and RelLTH exhibited modest and non-significant positive genetic correlations with all three area-

weighted wood densities (AwED, AwLD and AwDtot; r_A=0.10 to 0.37), with RelLTH having the strongest correlations. Likewise, Hannrup et al. (2001) reported for Scots pine a weak genetic correlation between fibre length and whole ring density (r_A=−0.09 to 0.20) for various age classes. However, in the literature review that included 14 references on fibre length in radiata pine, Wu et al. (2008) did not mention any reports presenting a significant genetic correlation between fibre length and wood density. Moreover, for white spruce Lenz et al. (2010) showed negative genetic correlation for the relationship density–radial fibre diameter (r_A=−0.36), while density showed positive genetic correlation with tangential fibre diameter (r_A=0.62), but negative again between density and height growth (r_A=−0.72). The studies referred to above have used different techniques, each of them including several steps for fibre analysis, and it is thus reasonable to assume that these differences had an impact on the results obtained. The challenge is to choose a technique with a capacity high enough to allow many samples to be analysed, thus making it possible to estimate genetic parameters with adequate precision. Optical analyzers for fibre length measurements seem to have limitations when used on fibre suspensions from 5-mm increment cores. This is demonstrated by the very high phenotypic coefficients of variation observed in this work (Table 1) and the modest responses to selection in spite of reasonably high heritabilities (Table 3). Using image analyses as a complement could however increase the precision of the optical data. Separating radial and tangential fibre diameter should also be considered, but this is probably not possible for fibre suspensions.

4.3 Genetic gains and correlated responses

A basic selection criterion in Scots pine breeding is height growth and the present results indicate a correlated response of between CR=−1 % and CR=−2 % in wood density at a 10 % selection for height (Table 3). Under selection for stem diameter, the negative response in wood density will be larger, with correlated responses of between −2.9 % and −3.9 %. According to Hannrup et al. (2000), who studied similar annual ring intervals in Scots pine, the correlated response in whole ring wood density for annual rings 9–20 from the pith was identical to that for rings 21–26 when selecting for height; CR=0.2 %. Based on this, a reasonably stable response may be expected from this age and to older ages. The negative correlated response in both AwED and AwLD (and thus also AwDtot) is in accordance with negative correlations found in Hannrup et al. (2000), Ivkovich et al. (2002b) and Fries and Ericsson (2009). The general pattern is thus that breeding for high growth capacity may generate wood with a slightly lower density. However, the correlations are modest, which suggests that selection for height will not seriously reduce biomass production.

It is shown in Fig. 2 that the negative effect on both earlywood and latewood densities remain when as large fraction as 50 % of the highest trees are selected; the reduction in both AwED and AwDtot is nearly 1 % (ca. 0.6 % for AwLD). Figure 2 shows also that the change in AwDtot in the present study should be ca. −0.33 % per percent change in height, and this is similar to the −0.2 % per percent change for annual rings 9–20 and 21–26 from pith that was stated in Hannrup et al. (2000). In contrast to the present results showing a reduction in RelLTH when selecting for height (−0.2 % per percent height increase), Hannrup et al. (2000) reported an increase by 0.3 % when selecting for height.

A slight positive correlated response in WTH when selecting for height was identified in this work ($CR_{h01,WTH}$=1.0 % at a 10 % height selection), while RelLTH would be expected to decrease slightly under height selection: $CR_{h01,RelLTH}$=−0.8 %. In contrast, according to Hannrup et al. (2000), fibre length should respond positively to selection for height, increasing by 0.3 % at approximately the 24th annual ring from the pith per percent increase in height. Furthermore, Ukrainetz et al. (2008) showed that in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), fibre coarseness (a trait that exhibits a strong genetic correlation with fibre length, cf. Pot et al. (2002)) seems to react positively to selection for height ($CR_{h01,coarseness}$=+0.59 % when selecting the 6.6 % highest trees). As with the genetic correlations, the differences between the reported correlated responses to height selection demonstrate that accurately measuring fibre lengths is difficult, especially when using automated optical methods.

5 Conclusions

In summary, it seems that it is possible to exert some degree of independent control over growth traits, fibre width and the densities of earlywood and latewood. However, it will probably be difficult to achieve simultaneous desirable changes in these traits (better growth, thinner but longer fibres and higher density) due to the numerous negative genetic correlations, especially between growth traits and wood density. Similar conclusions were drawn by Ivkovich et al. (2002b), Fries and Ericsson (2006; 2009) and Lenz et al. (2010). Breeding should therefore focus on improving adaptation, productivity, and stem and branch quality without unduly reducing wood density or adversely affecting fibre traits. One possibility is to use the approach discussed by Greaves et al. (1997) and Berlin (2009), which centres on developing indices for the different traits and assigning economic weights to specific traits to optimize the design

of selection strategies. Alternatively, it would be possible to identify and utilize families that deviate from the reported correlations ("correlation breakers") and combine, e.g. high production and high wood density, as described by Zubizarreta Gerendiain et al. (2007). When analysing fibre dimensions, one should choose a method with a high level of precision and which simultaneously can handle suitable sample sizes; 5-mm increment cores have the advantage that they can be obtained relatively quickly, include many annual rings and can in principle be obtained non-destructively, which make them possible to use for evaluation of progeny trials before the trial has reached the age for final evaluation. They however reduce the precision of the measurements, especially of fibre length. Optical fibre dimension analyzers can be used for large samples, but yield results with reduced precision due to damaged fibres, fibres that are attached to one-another or due to other wood particles. The precision of the measurements could, however, be increased by using image analyses to complement the optical data.

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