RELATIONSHIPS BETWEEN WOOD DENSITY AND TRACHEID DIMENSIONS IN *PINUS SYLVESTRIS* L.

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ABSTRACT

This study aimed at: (1) investigating the relationships between wood density and tracheid dimensions, (2) evaluating to what extent different cross-sectional dimensions could explain the genetic age-age correlations earlier estimated in the same progeny trial. The tracheid cross-sectional dimensions, radial and tangential lumen diameter, and cell-wall thickness were measured on increment cores collected in a progeny trial in southeastern Sweden. The measurements of tracheid dimensions were made with an automated method using image analysis. Data of wood density and tracheid length were taken from a previous study of the same progeny trial. The genetic control was strong for both radial and tangential lumen diameter of the earlywood, moderate for latewood proportion, and low for cell-wall thickness. Earlywood radial and tangential lumen diameter and latewood proportion showed the strongest correlations with wood density. Multiple regression analyses indicated that earlywood radial lumen diameter and latewood proportion were the two most important predictors of wood density, explaining between 24 and 73% of the variation in this trait. The strong genetic age-age correlations for wood density found in the previous study were suggested to be explained by earlywood radial and tangential lumen diameter, which showed positive and significant age-age correlations between family means.

Keywords: Wood density, tracheid cross-sectional dimensions, genetic correlation, image analysis.

INTRODUCTION

The dimensions of the tracheids of coniferous wood are the most important parameters in determining the properties of pulp and paper products (reviewed by Dinwoodie 1965). Among the different morphological traits, tracheid length is the most frequently studied, showing a positive relationship with tear strength of paper (e.g., Ericson et al. 1973; Kibblewhite et al. 1997; Marklund et al. 1998). Among the cross-sectional tracheid dimensions, cell-wall thickness is a good predictor of paper handsheet properties. For example, strong negative correlations ($r < -0.7$)

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have been observed between mean cell-wall thickness and tensile index (index is the ratio of an assessed variable to the weight of the paper per unit area), burst index, and apparent density (Kibblewhite 1997), whereas a positive correlation was found between cell-wall thickness and tear index (Kibblewhite et al. 1997). Measures related to the lumen diameter of the tracheids appear to be less important for fiber products, but Einspahr et al. (1969) and Kibblewhite et al. (1997) showed a negative impact of earlywood tracheid diameter and tracheid perimeter, respectively, on tear index.

In spite of their great impact on the end-products, tracheid dimensions are rarely included in tree-breeding programs. As a substitute, wood density has been included. This trait also shows a strong relationship with end-products and in addition is easier to measure. Furthermore, wood density shows strong genetic age-age correlations between juvenile and mature wood, indicating that selection can be efficient at a low tree age, e.g., *Pinus sylvestris* (Hannrup and Ekberg 1998). In conifers, however, wood density is a complex trait that is determined mainly by the proportion of earlywood and latewood, the cell-wall thickness, and the lumen diameter in the radial and tangential direction within the earlywood and latewood. The tracheid length may also influence the wood density, as shorter cells have a higher proportion of cell ends, but this effect is considered small as the tracheid length exceeds the tracheid diameter by a factor of 100.

Different studies of the relative importance of different tracheid dimensions on wood density are difficult to compare, since different variables are measured owing to the different measurement techniques used. Species differences also exist. In *Pinus radiata* (Donaldson et al. 1995) and in *Picea mariana* (Zhang and Morgenstern 1995), the earlywood density had the strongest impact on wood density, followed by latewood proportion and latewood density. This is in contrast to *Pinus taeda,* in which latewood proportion and latewood density (Hodge and Purnell 1993) or latewood proportion and latewood cell-wall thickness (van Buijtenen 1964) had the strongest influence on wood density. In *Picea sitchensis,* the variation in wood density at age 25 was best explained by the radial tracheid diameter, followed by the tangential tracheid diameter and the double cell-wall thickness (Mitchell and Denne 1997). In *Picea abies,* good agreement was observed between wood density and the combined effect of latewood proportion and earlywood radial tracheid diameter (Lindström 1997).

In Sweden (e.g., Vollbrecht 1996) and elsewhere (McNeely 1994), it has been proposed that some reforestation sites should be used for intensive plantation forestry with the primary aim of producing fibers for the pulp and paper industry. In such a production system, tree breeding can be an important component if a special type of fiber or composition of fibers can be identified as a production target. In such a situation, it may not be sufficient to select for wood density only but also include the different cross-sectional dimensions of the tracheids such as lumen diameter and cell-wall thickness. However, if strong correlations exist between wood density and the tracheid dimensions, tree breeding should focus on wood density only.

The aim of the present study was to investigate the relationships between wood density and the tracheid dimensions, radial and tangential lumen diameter, cell-wall thickness, and tracheid length in *Pinus sylvestris.* A second aim was to evaluate whether these tracheid dimensions could explain the high genetic age-age correlations for wood density earlier estimated in the same progeny trial (Hannrup and Ekberg 1998).

MATERIALS AND METHODS

Materials

A 33-year-old (age from seed) *Pinus sylvestris* progeny trial, located at Norra Kvill in southeastern Sweden at lat. 57°44'N, long. 15°33'E, and altitude 140 m, was used in this study. The progeny trial included 106 full-sib families from controlled matings between 30 parent trees, among which 26 trees served exclusively as females and 4 trees both as fe-

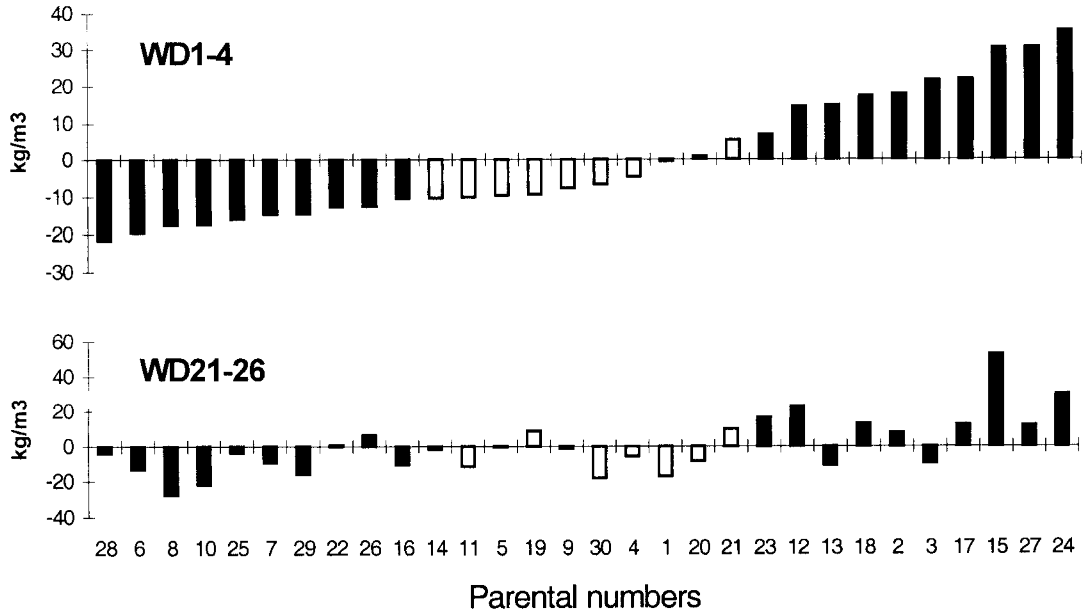

FIG. 1. Estimated breeding values of 30 parent trees for wood density at age 1–4 and 21–26. The parent trees are ranked according to their breeding values at age 1–4. In this study sampling were made among the progeny of the 20 parent trees with filled bars.

males and males. These latter trees were randomly sampled among the parent trees. No selfs were included. The original spacing was 1.4 m × 1.4 m and the 3-year-old seedlings were randomized in noncontiguous single-tree plots in 10 blocks. The trial is further described in Hannrup et al. (1998).

Sampling of materials

Two samplings of increment cores were made. In the first sampling, 10-mm increment cores were taken from a total of 948 trees from 106 families in 10 blocks. The increment cores were taken at 1.3 m at a 90° angle to the prevailing wind direction (southwest) to avoid reaction wood. These cores were used primarily for estimation of genetic parameters of wood density and tracheid length, and the results are reported in Hannrup and Ekberg (1998) and Hannrup et al. (1998). In the second sampling, cross-sectional tracheid dimensions were studied. As these dimensions are expensive to measure, the second sampling was a subsample. Twenty parent trees, ten with the highest and ten with the lowest breeding values for juvenile wood density, were selected (Fig. 1). Among these parent trees, 80 progenies were sampled from two blocks. From each of these trees, a 5-mm increment core was taken as close as possible to the previous sampling point.

Measurements

Juvenile cross-sectional tracheid dimensions were measured on the 3rd and 4th year ring from the pith. Mature dimensions were measured on year rings 2–7 from the bark, which corresponded approximately to ring 21–26 from the pith. The ring number counted from the pith differed slightly between the samples as the trees differed in the time needed to reach 1.3 m. For convenience, ring number from the pith is denominated as age throughout the text. The measurements of cross-sectional tracheid dimensions were made using an automated method that is briefly presented below and fully described by Moëll and Borgefors (1998) and Moëll and Borgefors (manuscript). After removal of extractives with acetone and ethanol, the increment cores were soaked in water and frozen. This treatment was followed by microtome cutting. Care was taken to orientate the cores perpendicular to the longitudinal direction of the tracheids to ensure that true cross-sectional surfaces of the wood were achieved. Digital images were taken along the increment cores using an integrated system consisting of a confocal microscope (TSM 4448, Noran Instruments, Wisconsin, USA) equipped with an auto stage (Prior H134BHNP, Prior Scientific Instruments, UK), a monochrome CCD-camera (COHU 8420, USA), and a computer equipped with a framegrabber. The images had 8-bit gray-levels and a size of 640 × 478 pixels, which equaled 553 × 413 μm as one pixel represented 0.86 μm. Each image contained approximately 14 radial cell files as the tracheids had an average tangential diameter of 30 μm. The measurements were made on the images with an image analysis program implemented as part of the IMP software (Nordin 1997), developed at the Center for Image Analysis, Uppsala, Sweden. The program automatically rotated the images so that the X-direction of the images was parallel to the radial cell files (to avoid problems with leaning year rings). The individual cells were identified, and on each cell the following variables were measured: lumen diameter in the radial and tangential direction and cell-wall thickness in the radial direction (Fig. 2). Cell-wall thickness of a single cell was measured on both cell walls in the radial direction, and the mean value of these two measurements was used as an observation.

Data on wood density and tracheid length were obtained from the first sampling step (Hannrup and Ekberg 1998). Wood density was measured at age 1–4 and 21–26 and tracheid length at age 4 and 24.

Computed variables

A preliminary analysis was performed in which the automated image analysis method using confocal microscope images was compared with the manual measurements using light microscopy. The comparison indicated that the image analysis program systematically overestimated cell-wall thickness and underestimated lumen diameter, when using light microscope measurements as a reference. Hence, the cell-wall thickness was reduced by 1.2 μm, and 2.4 μm was added to the radial and tangential lumen diameter. A detailed investigation of the performance of the image analysis method and a comparison with manual measurements on confocal microscope images will be presented in Moëll et al. (manuscript, in prep.).

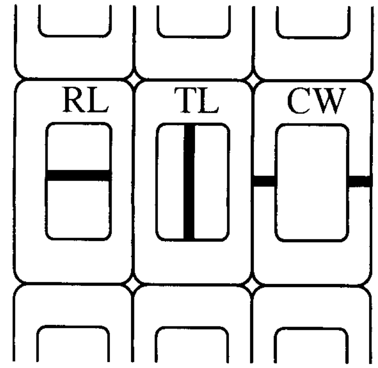

FIG. 2. Diagram showing three radial cell files and the bold lines indicate the measurements performed by the image analysis program. RL = radial lumen diameter, TL = tangential lumen diameter, and CW = cell-wall thickness.

Depending on the quality of the images, the number of measurable cells varied between the images. If there had been a systematic variation in the quality of the images, this would have biased the total mean values calculated. To avoid any such potential bias, the mean values of all variables were calculated for every 60-μm interval in the radial direction. These mean values were used in the further calculations.

Mean values of earlywood, latewood, and totally (i.e., mean of all measured cells) for radial lumen diameter, tangential lumen diameter, and cell-wall thickness were calculated for ring 3–4 and 21–26 (Table 1). To delimit the latewood, the original definition proposed by Mork (1928) was used, i.e., when twice the double wall thickness is greater than or equal to the lumen diameter.

TABLE 1. *Unit of measurement, mean values and coefficient of variation for total radial lumen diameter (TRL), earlywood radial lumen diameter (ERL), latewood radial lumen diameter (LRL), total tangential lumen diameter (TTL), earlywood tangential lumen diameter (ETL), latewood tangential lumen diameter (LTL), total cell-wall thickness (TCW), earlywood cell-wall thickness (ECW), latewood cell-wall thickness (LCW) and latewood proportion (LP) for year rings number 3–4 and 21–26, wood density (WD) for year rings number 1–4 and 21–26 and tracheid length (TL) for year ring number 4 and 24. There were 69 observations for the variables of the lower ages and 73 observations for the variables of the higher ages.*

Trait		Unit	Mean	CV %
TRL	3–4	μm	24.7	6.5
	21–26	μm	22.2	8.3
ERL	3–4	μm	25.8	6.2
	21–26	μm	29.3	6.2
LRL	3–4	μm	13.6	17.3
	21–26	μm	12.3	8.5
TTL	3–4	μm	21.3	6.9
	21–26	μm	20.7	6.9
ETL	3–4	μm	21.8	6.6
	21–26	μm	24.3	6.5
LTL	3–4	μm	16.3	11.6
	21–26	μm	15.6	7.4
TCW	3–4	μm	4.0	6.8
	21–26	μm	5.4	6.6
ECW	3–4	μm	3.9	6.6
	21–26	μm	4.6	6.2
LCW	3–4	μm	4.9	7.1
	21–26	μm	6.6	6.8
LP	3–4	%	9.5	47
	21–26	%	42	14.9
WD	1–4	kg/m³	368	7.2
	21–26	kg/m³	492	6.4
TL	4	mm	1.78	7.3
	24	mm	3.23	7.2

Statistical analyses

Owing to the low quality of the digital microscope images, some increment cores were rejected, resulting in a sample size of 69 and 73 trees at age 3–4 and 21–26, respectively. All the variables included in the statistical analyses are shown in Table 1. To study the fixed effects of parent and block on the different tracheid dimensions, an analysis of variance was performed using Proc Glm in SAS software (SAS 1996). A multivariate approach was used to group the tracheid cross-sectional variables using Proc Varclus (SAS 1996). The set of tracheid cross-sectional variables were divided into disjoint clusters, each cluster being a linear combination of the entered variables. The clustering was performed separately for the variables of the two ages studied. Multiple linear regressions were performed with Proc Reg (SAS 1996) to study the relative importance of the different tracheid dimensions for wood density. The best model containing one variable, two variables, etc. was analyzed using the criterion of adjusted R^2 (SAS 1996). Further variables were included as long as the probability-values of the included variables were below 0.10. Two different types of statistical models were used.

Model 1, parental means: $\tilde{\mathbf{y}} = \tilde{\mathbf{X}}\mathbf{b} + \mathbf{e}$, where $\tilde{\mathbf{y}}$ is the vector of observations of the dependent variable, i.e., mean values of wood density per parent at the ages studied, $\tilde{\mathbf{X}}$ is the design matrix with the independent variables, i.e., the mean values per parent of the different tracheid dimension(s), $\mathbf{b}$ is a vector of the parameters to be estimated, and $\mathbf{e}$ is the vector of random residuals. It is assumed that $E[\mathbf{e}] = \mathbf{0}$ and $Var[\mathbf{e}] = [\mathbf{I}\sigma^2_e]$.

Model 2, individual values: $\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{e}$, where individual tree values are used as observations instead of parental means. The same assumptions hold for the residuals as in Model 1, but it should be noted that the assumption of zero covariances between the residuals is violated as there are genetic covariances caused by common parents.

RESULTS AND DISCUSSION

Mean values of the tracheid dimensions and wood density

The total radial and tangential lumen diameter decreased with the age of the wood (Table 1). This is almost certainly an effect of the increasing proportion of narrow, thick-walled latewood tracheids. Within the earlywood, the radial and tangential lumen diameter increased with the age of the wood, which agrees with the age-trend normally occurring in conifers (e.g., Bannan 1965). The tangential lumen diameter was consistently smaller in the latewood than in the earlywood. This is partly explained by the thicker cell walls in the latewood, but another reason may be that the anticlinal cell divisions are limited to the latewood (Jackson and Morse 1965). For rings close to the pith, anticlinal divisions are not limited to the latewood (Bannan 1963, 1965), which is supported by this study in which the difference between earlywood and latewood tangential lumen diameter was smaller at age 3–4 than at age 21–26. The mean value of total radial tracheid diameter (TRL + 2 × TCW) found in this study at age 3–4 and 21–26 (Table 1) corresponded well with another study in *Pinus sylvestris* of corresponding ages (Atmer and Thörnqvist 1982). Studies not separating individual rings, but using a mixture of wood of similar age as in this study, report a mean tracheid diameter of 32 μm (Ericson et al. 1973, Fig. 20; Persson 1975, Fig. 74) which agrees well with the mean values obtained in this study. However, considerably higher values of earlywood radial tracheid diameter (47 μm) at age 5 have been reported in *Pinus sylvestris* (Persson et al. 1995, Fig. 4).

Genetic effects

Analysis of variance revealed no significant differences (P = 0.19–0.65) between parent trees for cell-wall thickness in the earlywood or latewood or at any of the ages studied (Table 2). In contrast, significant parental differences ($P \leq 0.03$) were obtained for radial and tangential lumen diameter in the earlywood at both ages and in the latewood at age 21–26. For latewood proportion, the differences between parents were significant at age 3–4 and nearly significant (P = 0.07) at age 21–26. This indicates a stronger genetic control of radial and tangential lumen diameter than of cell-wall thickness, where the genetic effect tended to be low. Moderate genetic control was indicated for latewood proportion. Only a few estimates of heritability for tracheid dimensions (except for latewood proportion) using a satisfactory sample size have been published. In *Pinus radiata,* Shelbourne et al. (1997) obtained high heritabilities for the

TABLE 2. *Results of the analysis of variance and the cluster analysis. Coefficient of determination of the model used and probability-values of block and parental effects for the different cross-sectional tracheid dimensions used as dependent variables. Clustering of the variables was performed separately at the two ages studied. Two clusters were obtained, denoted 1 and 2.*

Dependent variable[1]	R^2	p-value (block)	p-value (parent)	Cluster (3–4)	Cluster (21–26)
ERL3–4	0.45	0.67	0.02	1	
21–26	0.42	0.41	0.03		1
LRL3–4	0.39	0.10	0.13	2	
21–26	0.42	0.60	0.02		1
ETL3–4	0.57	0.34	0.0004	1	
21–26	0.47	0.06	0.01		1
LTL3–4	0.34	0.22	0.27		
21–26	0.46	0.23	0.01	2	1
ECW3–4	0.35	0.08	0.29		
21–26	0.34	0.38	0.19	2	2
LCW3–4	0.32	0.05	0.50		
21–26	0.25	0.26	0.65	2	2
LP3–4	0.45	0.35	0.03		
21–26	0.39	0.14	0.07	2	2

[1] See Table 1 for an explanation of the traits.

cross-sectional tracheid dimensions studied where radial tracheid diameter showed the highest heritability (h^2 = 0.67) followed by cell-wall thickness (h^2 = 0.56) and tangential tracheid diameter (h^2 = 0.37). The high heritability obtained for cell-wall thickness is not supported by the results in the present study. This may be due to species differences, but another explanation may be that no distinction was made between cell-wall thickness in the early- and latewood. Therefore the variation in cell-wall thickness also reflected the variation in latewood proportion. The moderate genetic control of latewood proportion found in this study agrees with the heritabilities published for this trait (e.g., Vargas-Hernandez and Adams 1991; Zhang and Morgenstern 1995).

The clustering of the tracheid cross-sectional dimensions was performed separately for the two ages studied, and at each age two clusters were obtained (Table 2). The biological interpretation of this clustering may be that variables showing strong genetic effect, as indicated by the significant parental differences, were separated from the others. This was true for both ages, with the exception of latewood

TABLE 3. *Pairwise correlations based on parental means and individual values between wood density and the tracheid dimensions at age 3–4 and 21–26.*

Tracheid dimension[1]	Parental means[2]		Individual values[2]	
	WD1–4	WD21–26	WD1–4	WD21–26
ERL	−0.43***	−0.59***	−0.44***	−0.25***
LRL	−0.05	0.16	0.13	−0.01
ETL	−0.16	−0.42***	−0.25***	−0.20*
LTL	−0.06	−0.12	−0.06	−0.14
ECW	−0.38***	0.21	0.00	0.11
LCW	0.19	0.01	0.15	0.08
LP	0.28	0.55***	0.35***	0.32***
TL	0.20	−0.09	0.06	0.01

[1] See Table 1 for an explanation of the traits.
[2] Significance levels: * $P < 0.05$, *** $P < 0.001$.

proportion at age 3–4, which showed significant parental differences but was grouped in the same cluster as the variables showing no significant parental effects.

Relationships between tracheid dimensions and wood density

Earlywood radial and tangential lumen diameter and latewood proportion showed significant correlations with wood density in all or most cases (Table 3). The importance of these three variables for wood density was confirmed in the multiple regression analyses. Inclusion of additional independent variables to earlywood radial lumen diameter and latewood proportion did not substantially improve the model fitting (Table 4), except for the regression based on parental means at age 3–4. Despite its significant correlations with wood density (Table 3), earlywood tangential lumen diameter did not enter into any of the regression models (Table 4). This may be caused by the significant correlation with earlywood radial lumen diameter (data not shown) indicating that when included together in the regression model, these two variables acted in a similar way to explain the variation in wood density.

The sample size in the present study was too small to make estimation of genetic parameters meaningful. However, the correlations presented using parental means and individual values are indications of the genetic and phenotypic correlations, respectively. The correlations based on parental means were

TABLE 4. *Results of the multiple regressions between wood density and tracheid dimensions based on parental means and individual values at age 3–4 and 21–26. Adj. R^2 is the coefficient of determination of the model which is adjusted for the number of independent variables included in the model.*

Parental means		Individual values	
Indep. variable(s)[1]	Adj. R^2	Indep. variable(s)[1]	Adj. R^2
	Age 3–4		
ERL	0.14	ERL	0.16
ECW, LCW	0.30	ERL, LP	0.24
ECW, LCW, LP	0.46	ERL, LCW, LP	0.25
ERL, ECW, LTL, LCW	0.59	ERL, ECW, LCW, LP	0.28
	Age 21–26		
ERL	0.60	LP	0.41
ERL, LP	0.73	ERL, LP	0.47
ERL, LP, TL	0.79	ERL, LCW, LP	0.52
ERL, LCW, LP, TL	0.82		

[1] See Table 1 for an explanation of the traits.

generally stronger, but the two types of correlations showed the same trend (Table 3). Both types of correlations indicated that the main effect on tracheid dimensions, following a selection for wood density, will be a decreased lumen diameter in the earlywood and a higher proportion of latewood. For fiber products, a decreased earlywood lumen diameter would mean an increased tearing strength (Einspahr et al. 1969; Kibblewhite et al. 1997) and probably a lower burst and tensile strength as the more narrow tracheids would be less prone to collapse during paper formation and consequently form fewer bonds between the fibers. An increased latewood proportion would affect the paper properties in a similar way, i.e., increase tearing strength and decrease burst and tensile strength. To sum up, the results indicated that it was earlywood radial and tangential lumen diameter and latewood proportion that showed the strongest relationship with wood density. These variables are suggested to be the basic factors behind the correlations obtained between wood density and fiber products reported (e.g., Einspahr et al. 1969; Ericson et al. 1973; Kibblewhite et al. 1997).

The tracheid dimensions were less good predictors of wood density at age 3–4 than at age 21–26 (Table 4). The use of a chemical reagent (sulfanilic acid + sodium nitrite) on a number of test cores showed that some trees had heartwood in the first annual rings. The heartwood increases the wood density but does not affect the tracheid dimensions. This result, together with the fact that wood density was not measured at the same age interval as the tracheid dimensions, may explain the weaker relationships observed at the lower age studied.

Age-age correlations

Positive and significant age-age correlations ($P \leq 0.004$) between parental means were observed for earlywood radial and tangential lumen diameter and wood density (Table 5). A significant negative correlation was shown for latewood radial lumen diameter, whereas the age-age correlations for the other tracheid dimensions were low and nonsignificant. For wood density, the correlation between age 1–4 and 21–26 was slightly weaker than the genetic age-age correlation ($r_A = 0.88$) estimated in the same progeny trial by Hannrup and Ekberg (1998). As no measurements were made on cross-sectional tracheid dimensions in the previous study, the basic factors behind the high age-age correlation could not be revealed. However, the results from the present study indicate that the two earlywood lumen diameters were the basic factors behind the high genetic age-age correlation for wood density. The significant negative age-age correlation for latewood radial lumen diameter is difficult to explain but may to some extent depend on the small proportion of latewood at age 3–4. Unexpectedly low age-age correlations were found for latewood proportion (Table 5). However, latewood proportion depends on several factors such as initiation and cessation of the annual cambial activity, the timing of the transition between early- and latewood formation and the growth rate of the cambium within the periods of early- and latewood formation.

TABLE 5. *Age-age correlations between parental means and probability values for the cross-sectional tracheid dimensions and wood density at age 3–4 and 21–26.*

Traits[1]	r	p-value
ERL3–4–ERL21–26	0.61	0.004
LRL3–4–LRL21–26	−0.54	0.01
ETL3–4–ETL21–26	0.74	0.0002
LTL3–4–LTL21–26	0.33	0.16
ECW3–4–ECW21–26	−0.13	0.57
LCW3–4–LCW21–26	−0.01	0.96
LP3–4–LP21–26	−0.22	0.35
WD1–4–WD21–26	0.73	0.0003

[1] See Table 1 for an explanation of the traits.

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