TWO SCALES OF VARIATION IN NORWAY SPRUCE TRACHEID PROPERTIES

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ABSTRACT

Variation in Norway spruce (*Picea abies*) tracheid properties is studied on two different scales: within and among specimens consisting of five annual rings. Within-specimen variation dominates the overall variability within a genotype. An exception is the variation in tracheid length, which is stronger among specimens. All variables describing the size-scale of tracheids, as well as the *oblongness* of tracheids, are found to be interdependent among specimens. Cross-sectional circumference and cross-sectional *compactness* are negatively interdependent, particularly within specimens. The latter relationship becomes more pronounced with increased cambium maturity. Combinations of tracheid properties, achievable using different screening and fractionation techniques, are reported. Apart from wood classification, tracheid oblongness can be controlled by screening with respect to tracheid length. Tracheid compactness can be effectively controlled by hydrodynamic fractionation.

Keywords: Tracheid properties, within-specimen, among-specimens, *Picea abies*.

INTRODUCTION

The properties of softwood tracheids change within a tree horizontally, from the pith of the tree towards the periphery, and vertically, from the ground level to the top (Sanio 1872; Hartig 1892, 1898). Tracheid dimensions usually increase monotonically outwards from the pith, but the longest tracheids are found in the lower middle parts of the bole (Sanio 1872; Mork 1928; Helander 1933; Atmer and Thörnqvist 1982). This evolution in tracheid properties seems to be due to maturation, localized in the meristems (Olesen 1973; Sirviö and Kärenlampi 1998). In addition to the maturity of the meristems, tracheid properties depend on growth rate (Hakkila 1966; Olesen 1976, 1977; Zobel and van Buijtenen 1989). The apparent growth rate varies systematically in the course of maturity, while the actual growth rate depends on various external and internal factors. Maturity-independent growth rate effects on tracheid properties have been recently investigated (Sirviö and Kärenlampi 1998).

In the evaluation of properties of heterogeneous materials, the choice of Representative Volume Element (RVE) is of primary importance. It has to be selected to be large enough to average fluctuations below the scale of interest. In the references cited above, the RVE has been implicitly selected in order to average fluctuations within annual rings (cf. Bisset and Dadswell 1950; Jackson and Morse 1965; Fengel and Stoll 1973; Zobel and van Buijtenen 1989). Thus, the RVE should consist of a number of annual rings, preferably of an integer number. The smaller this integer, the more accurately variation between the RVEs represents variation between annual rings.

As is obvious from the above, both quali-

TABLE 1. *Total age, diameter (over bark) at breast height, and height of sample trees.*

	Series 1	Series 2			
	1	1	Stand 2	3	4
Tree	Age, a/Diameter, cm/Height, m				
1	135/22/23	60/15/17	63/21/20	99/20/20	35/20/16
2	130/28/24	57/13/14	60/27/24	157/22/18	36/23/16
3	129/42/28	61/17/18	63/25/20		37/18/16
4	90/23/19	60/16/19	60/23/20		36/16/14
5	73/30/23	62/15/15			58/21/18
6	89/48/28				34/17/16
7					35/19/18
8					33/26/20
9					35/17/15

tative and quantitative models for the among-specimens variation in tracheid properties are available. However, the value of such models for tracheid applications depends on the dominance of the among-specimens variation in relation to the total variation in tracheid properties.

Tracheid properties vary also within any growth ring (Bisset and Dadswell 1950; Jackson and Morse 1965; Fengel and Stoll 1973; Zobel and van Buijtenen 1989). We call this scale of variation *within-specimen variation* regardless of whether one or a few growth rings are considered. This scale of variation is certainly due to growth-seasonal changes in cambium activity, which in turn may be controlled by growth regulators, turgor pressure, amount and quality of light, etc.

The purpose of this paper is to clarify the relative role of within-specimen and among-specimens variation on the total variation in tracheid properties. Technical difficulty of separating and processing narrow annual rings exactly at their borders invites a compromise in the choice of the RVE. Our specimens will

consist of five annual rings each, such specimens being still small enough that evolution in cambium maturity within a specimen can be considered small. Thus, we will experimentally study variation within small wood specimens, as well as among the specimens. We assume that most of the within-specimen variation arises from the variation within annual rings, and most of the among-specimens variation arises from the variation among annual rings. We also intend to clarify interrelationships between different tracheid properties on these two scales of variation. The maturity and growth rate of the meristems contributing to the quality of production (Sirviö and Kärenlampi 1998), the relative role of the two scales may well depend on such factors.

First, two independent Norway spruce sample series are introduced. The overall magnitudes of variation within either scale, as well as interrelationships between tracheid properties, are then reported. The effect of maturity and physiological intensity (a maturity-independent measure of growth rate) on these factors is clarified separately for both scales of

TABLE 2. *Number of specimens within low, medium, and high subgroup, classified according to cambium maturity, apical maturity, and physiological intensity for both sample series.*

	Maturity						Physiological intensity		
	Cambium			Apical meristem					
Series	low	medium	high	low	medium	high	low	medium	high
1	18	20	21	13	10	36	27	28	4
2	32	13	26	30	16	25	13	36	22

TABLE 3. *The range of maturity and physiological intensity within low, medium, and high subgroup, classified according to cambium maturity, apical maturity, and physiological intensity for both sample series.*

	Maturity								
	Cambium			Apical meristem			Physiological intensity		
	low	medium	high	low	medium	high	low	medium	high
Series	*[kg/m]*			*[m]*			*[dimensionless]*		
1	0.0–0.8	0.9–5.7	6.0–40	1.3–2.6	4.4–8.6	10–26	0.2–0.9	1.0–2.0	2.9–3.9
2	0.1–0.6	0.7–2.7	3.4–13	3.0–3.0	6.0–6.0	9.0–15	0.1–0.5	0.6–1.2	1.2–2.2

variation. We then clarify how far the variation in tracheid properties within these experimental sample series may be due to different tree genotypes. Finally, combinations of tracheid properties, achievable using different kinds of wood classification and tracheid fractionation approaches, are addressed.

MATERIALS AND METHODS

Sample collection

Two sample series from Norway spruce (*Picea abies* (L.) Karst) trees were obtained from the interior of Southern Finland.

Sample series 1 was collected from six trees aged between 73 and 135 years, selected from one typical spruce stand in order to represent significantly varying growth-rate history: the breast-height diameter (dbh) varied between 22 and 48 cm. *Sample series 2* was collected from 20 trees, randomly sampled from four different stands, these stands representing different site fertility classes. The age of the trees varied between 34 and 157 years, and the dbh between 13 and 27 cm. More detailed description of sample trees is presented in Table 1.

In both cases, disks were cut at regular intervals in the longitudinal direction of the sample boles. For sample series 1, the disks were cut at intervals of 10 height-growth increments and for series 2 at intervals of 3 meters. The number of growth rings within any disk was counted, and their width was measured. Match-size specimens, consisting of 5 annual rings, were cut from the disks at intervals of 10 annual rings (rings 3–7, 13–17, . . . from the pith to the bark). In all, 259 and 205
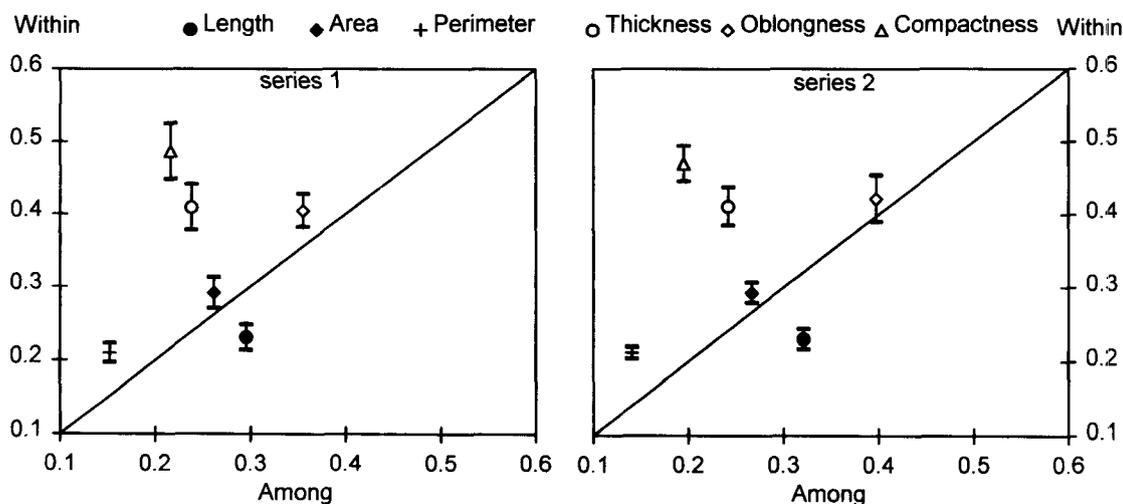

FIG. 1. Within-specimen and among-specimens coefficients of variation of tracheid properties. Vertical lines are the 95% confidence intervals for the within-specimen averages.

◆ Length-Thickness   ▲ Length-Perimeter   ■ Area-Perimeter

● Oblongness-Perimeter   ✱ Length-Area   ✕ Oblongness-Area

○ Area-Thickness   ◇ Oblongness-Length   △ Compactness-Length

□ Thickness-Oblongness   ✦ Compactness-Area   ― Perimeter-Thickness

▨ Compactness-Perimeter   ▴ Thickness-Compactness   ✛ Compactness-Oblongness
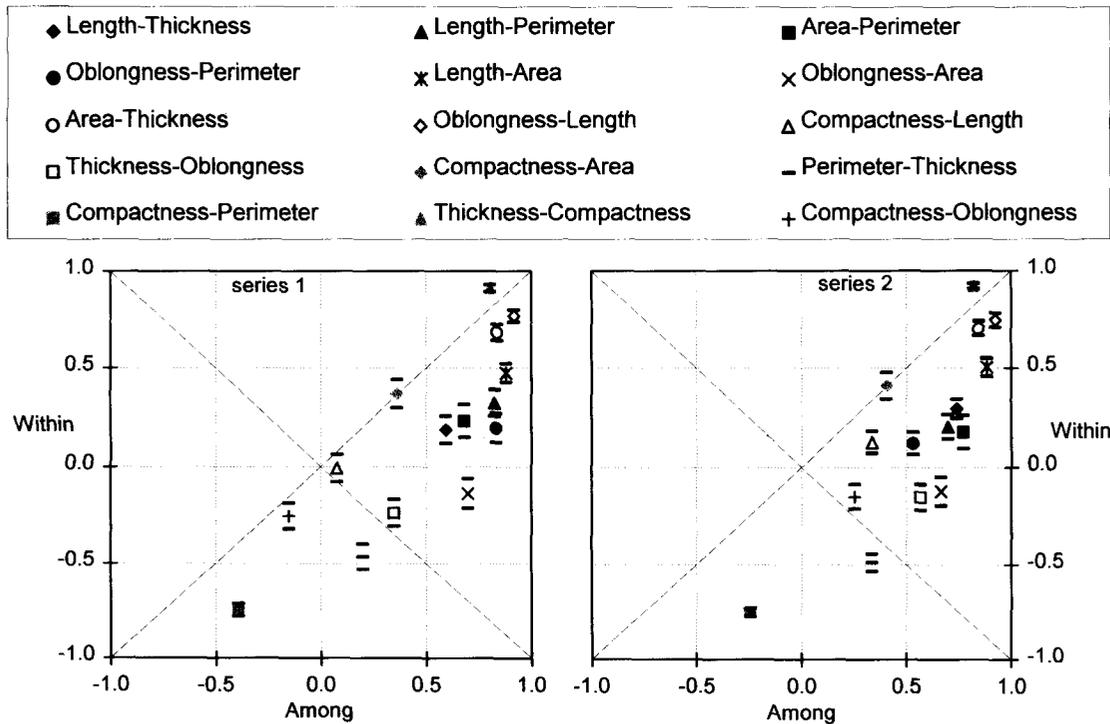
FIG. 2.   Coefficients of correlation between tracheid properties on among-specimens and on within-specimen scales. Short horizontal lines are the 95% confidence intervals for the within-specimen averages.

specimens, for series 1 and 2 respectively, were macerated in a mixture of glacial acetic acid and hydrogen peroxide (1:1 (vol.), 60°C, 24 h). Tracheid length and coarseness were measured using a commercial optical fiber quality analyzer. Air-dried ($+22$°C, 16% RH) tracheid specimens for confocal microscope analysis (see Jang et al. 1992; Moss et al. 1993) were prepared from at least every fourth wood specimen in order to achieve the same variation in maturity and growth-rate combinations as in original sampling. This resulted in 59 and 71 tracheid specimens for series 1 and 2 respectively. Confocal laser scanning microscope (clsm) images of tracheid cross sections of these specimens were produced perpendicular to the long axis of the tracheid, at a distance 35% of tracheid length from a randomly selected tracheid edge. The number of tracheids analyzed using confocal microscopy was about 1,000 for series 1 (17 ± 3 (mean±standard deviation) per specimen), and

1,400 for series 2 (20 ± 2 per specimen). The basic density of each sample was determined as oven-dry mass divided by green volume.

We refer to within-specimen variation when considering the variation within any sample, and among-specimens variation when referring to variation between the samples.

Tracheid properties

We will use two sets of variables to describe tracheid properties. Variables used to describe size scale are tracheid length, cross-sectional cell-wall area, tracheid perimeter (circumference), and cell-wall thickness. Besides these size-scale variables, scale-independent geometry variables are of interest. Tracheid oblongness is defined as $\pi L^2/(4A)$, where L is the tracheid length, and A is the cross-sectional cell-wall area. Cross-sectional compactness is defined as $4\pi A/P^2$, where P is the perimeter. The solid fraction of wood substance is de-

TABLE 4. *The within-species coefficients of variation of tracheid properties within each subgroup of cambium and apical maturity, and physiological intensity, for both sample series. Subgroups are indicated as L = low, M = medium, and H = high. Subgroups indicated by similar special font types (italics or bold) had statistically significant differences (P < 0.05) according to paired t-test.*

| Property | Cambium maturity | | | | | | Apical maturity | | | | | | Physiological intensity | | | | | |
| | Series 1 | | | Series 2 | | | Series 1 | | | Series 2 | | | Series 1 | | | Series 2 | | |
	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
Length	*0.27*	**0.21**	*0.22*	*0.26*	**0.22**	*0.20*	**0.19**	**0.28**	**0.23**	0.22	0.22	0.25	0.22	0.25	0.20	*0.19*	**0.24**	*0.24*
Area	0.29	0.29	0.29	*0.27*	**0.32**	*0.31*	0.28	0.31	0.29	0.30	0.30	0.29	0.30	0.29	0.25	**0.32**	**0.30**	*0.27*
Perimeter	**0.20**	*0.19*	**0.24**	0.21	0.21	0.22	0.22	0.23	0.20	0.20	0.20	0.22	0.22	0.20	0.23	0.21	0.22	0.20
Thickness	*0.33*	**0.41**	*0.47*	*0.33*	**0.45**	*0.49*	0.46	0.43	0.38	**0.44**	*0.42*	*0.37*	0.44	0.38	0.36	**0.50**	**0.41**	0.36
Oblongness	0.41	0.40	0.40	0.44	0.43	0.39	0.37	0.46	0.40	0.41	0.41	0.45	0.40	0.41	0.37	0.40	0.41	0.45
Compactness	**0.38**	**0.50**	0.57	**0.40**	**0.50**	0.54	0.57	0.49	0.46	0.49	0.49	**0.43**	0.51	0.46	0.50	0.52	0.47	0.44

fined as ρ_w/ρ_{cw}, where ρ_w is the basic wood density, and ρ_{cw} is the basic cell-wall material density, 1.5 g/cm³ (Kellogg and Wangaard 1969; Kellogg et al. 1975).

Data analysis

The magnitude of variation in any property within a specified population is described using the *coefficient of variation* (CV), i.e., the standard deviation normalized by the mean. Interrelationships between different tracheid properties are explored using *coefficients of correlation* between the properties within any population. The coefficient of correlation was defined as Pearson's product moment correlation coefficient, which describes the linear relationship between the variables (Ranta et al. 1991).

In order to find out the influence of maturity and physiological intensity (maturity-independent growth rate) on variation, both of the sample series were divided into subgroups with respect to these factors. Maturity effects on tracheid properties are greatest within juvenile wood (Boutelje 1968; Olesen 1977; Yang and Hazenberg 1994). However, juvenile and mature wood are not easy to distinguish. Actually, the classification to juvenile and mature wood is artificial, since there is no abrupt threshold. Maturity effects on tracheid properties should be described as a continuous evolution. We have divided our data into three subgroups just for technical purposes; this enables analyzing eventual differences in the variation of tracheid properties as a function of controlling variables. Variables describing physical size appear to be more reliable indicators of maturity than variables describing chronological age (Longman and Wareing 1959; Robinson and Wareing 1969; Hackett 1976; Wareing and Frydman 1976; Olesen 1978). Thus, cambium maturity was represented by height mass, the height differential of bole biomass, and apical maturity was represented by height from the ground level. A dimensionless measure of physiological intensity was produced as the ratio of height-mass-

TABLE 5. *The within-specimen coefficients of correlation between tracheid properties within each subgroup of cambium and apical maturity, and physiological intensity, for both sample series. Subgroups are indicated as L = low, M = medium, and H = high. Subgroups indicated by similar special font types (italics or bold) had statistically significant differences (P < 0.05) according to paired t-test.*

Properties	Cambium maturity						Apical maturity						Physiological intensity					
	Series 1			Series 2			Series 1			Series 2			Series 1			Series 2		
	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
Length																		
Area	***0.6***	**0.4**	*0.4*	**0.6**	0.5	**0.4**	0.4	0.5	0.5	0.5	0.5	0.6	0.4	0.5	0.5	0.4	0.5	0.5
Perimeter	0.4	0.2	0.3	*0.3*	**0.1**	*0.1*	0.3	0.3	0.4	***0.1***	**0.2**	*0.3*	0.3	0.4	0.2	0.1	0.2	0.3
Thickness	0.3	0.2	0.1	0.3	0.3	0.3	0.1	0.3	0.2	0.3	0.2	0.3	0.2	0.2	0.2	0.3	0.3	0.3
Oblongness	***0.8***	**0.7**	*0.7*	***0.8***	**0.7**	*0.7*	0.7	0.8	0.8	0.7	0.8	0.8	**0.7**	**0.8**	0.8	***0.6***	**0.8**	*0.8*
Compactness	0.0	0.0	−0.1	0.1	0.2	0.1	−0.1	0.1	0.0	0.2	0.0	0.1	0.0	0.0	0.0	0.2	0.1	0.1
Area																		
Perimeter	***0.5***	**0.1**	*0.1*	***0.4***	**0.1**	−0.1	0.1	0.2	0.3	**0.1**	*0.1*	*0.3*	**0.1**	0.3	0.3	*−0.1*	0.2	*0.3*
Thickness	0.7	0.7	0.7	**0.6**	**0.7**	0.8	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.7	0.6	***0.8***	**0.7**	*0.7*
Oblongness	***0.1***	**−0.3**	*−0.2*	***0.1***	**−0.2**	*−0.3*	−0.3	0.0	−0.1	−0.2	−0.2	0.0	**−0.2**	**0.0**	−0.1	*−0.4*	−0.1	0.0
Compactness	***0.2***	**0.4**	*0.4*	***0.2***	**0.5**	*0.6*	0.4	0.4	0.4	0.5	0.4	0.3	0.4	0.3	0.2	***0.6***	**0.4**	*0.3*
Perimeter																		
Thickness	**−0.3**	**−0.5**	*−0.6*	**−0.4**	**−0.5**	−0.6	−0.6	−0.5	−0.4	−0.5	−0.5	−0.4	−0.5	−0.4	−0.5	−0.6	−0.5	−0.4
Oblongness	0.2	0.1	0.2	0.1	0.1	0.2	0.2	0.2	0.2	0.1	0.2	0.1	0.2	0.2	0.0	0.1	0.1	0.1
Compactness	**−0.7**	−0.8	**−0.8**	**−0.7**	−0.8	**−0.8**	*−0.8*	**−0.8**	*−0.7*	−0.8	−0.8	−0.7	−0.8	−0.7	−0.8	−0.8	−0.8	−0.7
Thickness																		
Oblongness	***0.0***	**−0.3**	*−0.4*	***0.0***	**−0.2**	*−0.3*	−0.4	−0.1	−0.2	−0.2	−0.2	−0.1	**−0.3**	**−0.2**	**−0.1**	*−0.4*	*−0.1*	*−0.1*
Compactness	***0.9***	**0.9**	*0.9*	***0.9***	**0.9**	*1.0*	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	1.0	0.9	0.9
Oblongness																		
Compactness	***−0.1***	**−0.3**	*−0.3*	***0.0***	**−0.2**	*−0.3*	−0.3	−0.2	−0.2	−0.2	−0.3	−0.1	−0.3	−0.2	−0.1	*−0.3*	**−0.1**	*−0.1*

increment rate in relation to the increment rate typical of that particular maturity (Sirviö and Kärenlampi 1998).

In practice, the logarithm of cambium maturity was taken first, and the observations within both sample series were divided into three subgroups linearly with respect to the logarithm of maturity. For consistency, the same procedure was used to divide the specimens into three subgroups with respect to apical maturity and physiological intensity. The number of specimens within any subgroup after this division is shown in Table 2, and the variation in maturity and physiological intensity in Table 3.

Variance analysis was used to estimate the statistical significance of differences between the two sample series, as well as between the subgroups within the sample series, for the within-specimen variation. If the variance analysis indicated differences between the subgroups, the analysis was continued by paired *t*-tests. For the analysis of among specimens variation, a slightly modified method was used (Sokal and Brauman 1980; Ranta et al. 1991).

In order to evaluate the relative importance of cambium and apical maturity and physiological intensity on the control of variation, stepwise nonlinear regression analysis technique was applied.

RESULTS AND DISCUSSION

Variation in tracheid properties within specimen and among specimens

Coefficients of variation of tracheid properties, except that of tracheid length, were higher within specimen than among specimens in both sample series (Fig. 1). No statistically significant differences ($P < 0.05$) appeared between the series. The within-specimen variation thus seems to dominate the overall variation, particularly in the case of cell-wall thickness and cross-sectional compactness.

To the best of our knowledge, no previous analyses of the relative importance of the magnitude of these two scales of variation are

available. However, some published data lend themselves to analysis (Hartig 1892; Mork 1928; Helander 1933; Atmer and Thörnqvist 1982), partially confirming the present findings (Fig. 1).

Most of the among specimens correlations between tracheid properties are positive (Fig. 2). Only the correlation between tracheid perimeter and cross-sectional compactness is negative, on both scales of variation. Correlations between cross-sectional cell-wall area and tracheid oblongness, cell-wall thickness and oblongness, and perimeter and cell-wall thickness are negative within specimen, but positive among specimens.

Most of the correlations are clearly stronger among specimens than within specimen (Fig. 2). The obvious explanation is that the size-scale of tracheids, as well as their oblongness, mostly increases with cambium maturity (Sanio 1872; Hartig 1898; Mork 1928; Atmer and Thörnqvist 1982; Sirviö and Kärenlampi 1998). Size-scale variables thus correlate positively with each other on the among specimens scale.

On the other hand, correlations between perimeter and compactness, perimeter and cell-wall thickness, and thickness and compactness are stronger within specimen (Fig. 2). This is obviously related to two previous observations. First, compactness and cell-wall thickness mainly vary within specimen (Fig. 1). Second, the cross-sectional geometry of tracheids, determining the wood basic density, mostly depends on growth rate, not cambium maturity (Hakkila 1966; Olesen 1976, 1977; Zobel and van Buijtenen 1989; Sirviö and Kärenlampi 1998).

Cross-sectional cell-wall area correlates more strongly with cell-wall thickness than with tracheid perimeter, particularly within specimen (Fig. 2).

It is worth noting that there is no within-specimen correlation between tracheid length and compactness (Fig. 2). Tracheid length does not change systematically with increasing compactness; in other words, "latewood" tracheids are not longer than "earlywood" tra-

TABLE 6A. *The among-specimens coefficient of variation of tracheid properties within each subgroup of cambium and apical maturity, and physiological intensity of both sample series. Subgroups are indicated as L = low, M = medium, and H = high. Subgroups indicated by similar special font types (italics or bold) had statistically significant differences (P < 0.05) according to paired t-test.*

Property	Cambium maturity Series 1 L	M	H	Series 2 L	M	H	Apical maturity Series 1 L	M	H	Series 2 L	M	H	Physiological intensity Series 1 L	M	H	Series 2 L	M	H
Length	0.23	0.12	0.15	0.11	0.23	0.12	0.17	0.29	0.33	0.31	0.33	0.33	0.24	0.31	0.15	0.07	0.30	0.28
Area	0.16	0.16	0.17	0.14	0.17	0.13	0.23	0.26	0.25	0.28	0.26	0.25	0.21	0.26	0.13	0.18	0.28	0.22
Perimeter	0.13	0.07	0.10	0.11	0.11	0.09	0.11	0.12	0.17	0.15	0.13	0.14	0.14	0.17	0.13	0.07	0.17	0.13
Thickness	0.13	0.21	0.22	0.14	0.23	0.18	0.26	0.25	0.20	0.25	0.26	0.21	0.18	0.20	0.09	0.18	0.22	0.13
Oblongness	0.30	0.20	0.19	0.21	0.34	0.25	0.18	0.31	0.42	0.42	0.39	0.35	0.29	0.40	0.18	0.16	0.34	0.31
Compactness	0.18	0.22	0.24	0.18	0.22	0.19	0.27	0.18	0.20	0.19	0.20	0.19	0.17	0.20	0.20	0.16	0.17	0.11
Solid fraction	0.14	0.09	0.13	0.09	0.16	0.18	0.13	0.06	0.14	0.15	0.10	0.08	0.12	0.10	0.06	0.17	0.09	0.08
Coarseness	0.24	0.15	0.14	0.25	0.17	0.20	0.17	0.25	0.24	0.29	0.31	0.31	0.20	0.26	0.11	0.25	0.28	0.26

cheids (cf. Mork 1928; Bisset and Dadswell 1950; Anderson 1951; Sirviö and Kärenlampi 1997).

Mainly the coefficients of correlation between tracheid properties were statistically the same between the sample series. However, on within specimen scale the correlation of tracheid length with tracheid perimeter, cell-wall thickness, and cross-sectional compactness, as well as that of tracheid oblongness with compactness, displayed statistically significant difference ($P < 0.05$) between the sample series. Anyway, these correlations were not high within either of the sample series. On between-specimens scale, the correlation of oblongness with perimeter, and compactness, was statistically different between the sample series. Still, in the former case the correlation was clearly positive within both of the series, and nonexistent in the latter case.

Effect of maturity and physiological intensity on within-specimen variation

Stepwise nonlinear regression analysis showed that the major mechanism affecting within-specimen coefficients of variation (CV) of tracheid properties was cambium maturity. The CV of tracheid length decreased with increasing height mass, whereas the CV of cell-wall thickness and cross-sectional compactness increased significantly (Table 4). In the case of these tracheid properties, juvenile wood (low cambium maturity) differed statistically significantly ($P < 0.05$) from mature and transition wood. Since these phenomena take place at any height within the tree, inverse phenomena are visible in the apparent effect of apical maturity; the greater the height within the bole, the smaller the height mass. Also growth rate seemed to affect the coefficients of variation, especially within sample series 2.

Stepwise nonlinear regression analysis showed that the major factor affecting the coefficients of correlation on the within specimen scale was cambium maturity. However, in the case of the correlation between tracheid

TABLE 6B. *The among-specimens coefficient of variation of tracheid properties within each subgroup of cambium and apical maturity, and physiological intensity, of both sample series, normalized with the overall coefficient of variation of any property within the corresponding sample series. Subgroups are indicated as L = low, M = medium, and H = high.*

Property	Cambium maturity						Apical maturity						Physiological intensity					
	Series 1			Series 2			Series 1			Series 2			Series 1			Series 2		
	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
Length	0.8	0.4	0.5	0.3	0.7	0.4	0.6	1.0	1.1	1.0	1.0	1.0	0.8	1.1	0.5	0.2	0.9	0.9
Area	0.6	0.6	0.6	0.5	0.6	0.5	0.9	1.0	1.0	1.0	1.0	0.9	0.8	1.0	0.5	0.7	1.0	0.8
Perimeter	0.9	0.7	0.5	0.8	0.7	0.6	0.7	0.8	1.1	1.1	0.9	1.0	0.9	1.1	0.8	0.5	1.2	0.9
Thickness	0.6	0.9	0.9	0.6	1.0	0.8	1.1	1.0	0.9	1.0	1.1	0.9	0.8	0.8	0.4	0.7	0.9	0.6
Oblongness	0.8	0.6	0.5	0.5	0.8	0.6	0.5	0.9	1.2	1.0	1.0	0.9	0.8	1.1	0.5	0.4	0.8	0.8
Compactness	0.9	1.0	1.1	0.9	1.1	1.0	1.2	0.8	0.9	1.0	1.1	1.0	0.8	0.9	0.9	0.8	0.9	0.6
Solid fraction	1.1	0.8	1.0	0.7	1.2	1.2	1.1	0.5	1.1	1.2	0.9	0.7	0.9	0.8	0.5	1.5	0.7	0.7
Coarseness	1.0	0.6	0.6	0.7	0.6	0.6	0.7	1.0	1.0	1.0	1.0	1.0	0.8	1.0	0.4	0.8	0.9	0.9

perimeter and cross-sectional compactness, apical maturity explained the variation better in both sample series.

Within-specimen coefficients of correlation between tracheid properties were significantly affected by cambium maturity (Table 5). The correlation between tracheid length and cross-sectional cell-wall area and tracheid oblongness decreased with maturity. Also the coefficient of correlation between cross-sectional cell-wall area and tracheid perimeter decreased. That between cross-sectional cell-wall area and oblongness became negative. The correlation between cross-sectional cell-wall area and compactness increased with maturity.

The correlation between tracheid perimeter and cell-wall thickness became considerably more negative with increasing maturity, as did that between perimeter and cross-sectional compactness (Table 5). With increasing maturity, negative correlations appeared between cell-wall thickness and tracheid oblongness, as well as between oblongness and compactness. Typically, the coefficients of correlation differed statistically significantly ($P < 0.05$) between juvenile wood and other wood types. Again, inverse phenomena are visible in the apparent effect of apical maturity; the greater the height within the bole, the smaller the height mass.

The positive correlation between tracheid length and oblongness became stronger with increasing physiological intensity, as did that between cross-sectional cell-wall area and tracheid perimeter (Table 5). The correlation between cross-sectional cell-wall area and oblongness became less negative with increasing physiological intensity, as did that between cell-wall thickness and oblongness. Typically, the lowest growth-rate group displayed statistically significant ($P < 0.05$) differences between other growth-rate categories.

Cell-wall thickness and cross-sectional compactness correlated strongly throughout the specimen sub-groups.

TABLE 7. *The among-specimens coefficients of correlation between tracheid properties within each subgroup of cambium and apical maturity, and physiological intensity, for both sample series. Subgroups indicated as L = low, M = medium, and H = high. Subgroups indicated by similar special font types (italics or bold) had statistically significant differences (P < 0.05) according to paired t-test.*

	Cambium maturity						Apical maturity						Physiological intensity					
	Series 1			Series 2			Series 1			Series 2			Series 1			Series 2		
Property	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
Length																		
Coarseness	0.5	0.6	0.7	0.6	0.8	0.5	0.7	0.9	0.8	0.7	0.8	0.8	0.8	0.7	0.6	0.8	0.9	0.8
Area	0.8	0.7	0.6	0.6	0.8	0.4	0.8	0.9	0.9	0.9	0.8	0.9	0.8	0.9	1.0	0.7	0.9	0.9
Perimeter	0.7	0.3	0.5	0.6	0.2	-0.2	0.6	0.8	0.9	0.7	0.6	0.9	0.9	0.9	1.0	0.8	0.8	0.9
Thickness	0.4	0.5	0.2	0.1	0.6	0.4	0.5	0.7	0.6	0.5	0.8	0.6	0.5	0.5	-0.3	0.2	0.7	0.7
Oblongness	0.9	0.6	0.8	0.6	0.9	0.8	0.6	1.0	1.0	0.9	0.9	0.9	0.9	0.9	0.8	0.2	0.9	0.9
Compactness	-0.2	0.3	0.0	-0.3	0.5	0.4	0.2	0.5	-0.1	0.4	0.5	0.1	-0.2	-0.2	-0.8	-0.2	0.0	-0.1
Solid fraction	-0.3	0.1	0.1	-0.1	0.6	0.5	0.0	0.7	-0.4	0.2	0.6	0.2	-0.7	-0.4	-0.6	0.2	-0.1	0.1
Coarseness																		
Area	0.4	0.8	0.7	0.3	0.9	0.7	0.8	0.9	0.8	0.9	0.9	0.8	0.9	0.7	0.7	0.9	0.9	0.7
Perimeter	0.4	0.2	-0.1	0.6	0.5	0.2	0.0	0.8	0.7	0.7	0.8	0.8	0.7	0.6	0.5	0.7	0.9	0.8
Thickness	0.2	0.7	0.6	-0.1	0.5	0.5	0.8	0.8	0.6	0.8	0.7	0.5	0.6	0.6	0.1	0.6	0.7	0.5
Oblongness	0.3	0.2	0.3	0.6	0.6	0.2	0.1	0.9	0.7	0.6	0.6	0.9	0.6	0.6	0.0	-0.2	0.8	0.8
Compactness	-0.1	0.5	0.5	-0.4	0.3	0.3	0.7	0.5	0.0	0.4	0.3	0.0	0.1	0.1	-0.4	0.3	0.0	-0.3
Solid fraction	-0.1	0.5	0.6	-0.2	0.4	0.6	0.6	0.6	-0.2	0.4	0.2	0.1	-0.4	0.0	0.3	0.4	-0.2	0.0
Area																		
Perimeter	0.8	0.1	0.0	0.6	0.4	0.3	0.3	0.7	0.8	0.8	0.8	0.8	0.7	0.8	0.9	0.6	0.8	0.9
Thickness	0.4	0.9	0.8	0.6	0.8	0.7	0.9	0.9	0.8	0.9	0.9	0.8	0.8	0.8	-0.1	0.8	0.8	0.9
Oblongness	0.8	0.1	0.1	0.1	0.5	-0.1	0.0	0.8	0.8	0.6	0.6	0.5	0.5	0.7	0.7	-0.4	0.8	0.7
Compactness	-0.2	0.7	0.6	0.6	0.6	0.4	0.6	0.7	0.1	0.4	0.5	0.3	0.2	0.1	-0.7	0.5	0.2	0.0
Solid fraction	-0.3	0.5	0.6	-0.1	0.5	0.6	0.4	0.7	-0.3	0.3	0.3	0.2	-0.4	-0.2	-0.4	0.6	-0.1	0.0
Perimeter																		
Thickness	-0.1	-0.4	-0.5	-0.3	-0.2	-0.4	-0.2	0.4	0.2	0.4	0.4	0.2	0.2	0.3	-0.5	0.0	0.4	0.6
Oblongness	0.7	0.5	0.6	0.5	0.1	-0.4	0.6	0.8	0.9	0.5	0.3	0.9	0.8	0.9	0.8	0.2	0.7	0.8
Compactness	-0.7	-0.6	-0.8	-0.7	-0.5	-0.7	-0.5	0.0	-0.5	-0.2	-0.1	-0.4	-0.5	-0.5	-0.9	-0.3	-0.3	-0.4
Solid fraction	-0.7	-0.4	-0.6	-0.5	-0.4	-0.2	-0.5	0.3	-0.7	-0.1	-0.2	-0.3	-0.8	-0.6	-0.6	0.2	-0.4	-0.1
Thickness																		
Oblongness	0.2	-0.1	-0.3	-0.2	0.5	0.1	-0.3	0.6	0.4	0.5	0.6	0.5	0.1	0.2	-0.4	-0.7	0.6	0.4
Compactness	0.8	1.0	0.9	0.8	0.9	0.9	0.9	0.9	0.7	0.9	0.9	0.8	0.7	0.7	0.8	0.9	0.7	0.5
Solid fraction	0.5	0.6	0.8	0.4	0.8	0.7	0.7	0.7	0.3	0.6	0.6	0.5	0.0	0.4	0.3	0.7	0.2	0.0

TABLE 7. *Continued.*

Property	Cambium maturity						Apical maturity						Physiological intensity					
	Series 1			Series 2			Series 1			Series 2			Series 1			Series 2		
	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H	L	M	H
Oblongness																		
Compactness	-0.3	-0.3	-0.4	*-0.4*	**0.3**	0.2	-0.5	0.4	-0.2	0.3	0.5	0.0	-0.5	-0.4	-0.7	**-0.8**	**0.1**	-0.4
Solid fraction	-0.3	-0.1	-0.4	-0.1	0.5	0.1	*-0.4*	*0.6*	*-0.5*	**0.1**	**0.7**	0.2	-0.8	-0.5	-0.9	*-0.7*	**0.0**	*0.2*
Compactness																		
Solid fraction	0.8	0.6	0.8	0.5	0.9	0.6	0.8	0.6	0.7	0.6	0.7	0.7	0.5	0.8	0.5	0.6	0.6	0.1

Effect of maturity and physiological intensity on among-specimens variation

The among-specimens coefficients of variation of tracheid properties for subgroups of different maturity or growth rate (Table 6a) appear to be less informative than the corresponding within-specimen coefficients. Typically, the lowest growth-rate group displayed statistically significant ($P < 0.05$) differences between other growth-rate categories within sample series 2. However, normalizing the coefficients of variation within the subgroups with the corresponding coefficient for the entire sample series (Table 6b) shows that in the case of size-scale variables of tracheids (except cell-wall thickness), dividing the specimens into subgroups according to cambium maturity significantly decreased the magnitude of variation. This is, naturally, a consequence of removing a major part of the systematic effect of maturity on tracheid properties. Correspondingly, the variability of cross-sectional compactness, solid fraction, and cell-wall thickness were reduced by dividing the specimens into subgroups with respect to physiological intensity, because of their heavy dependence on growth rate (cf. Sirviö and Kärenlampi 1998). Within average-growth-rate group (subgroup M), the variation seems to be as its highest.

The changes in the coefficients of correlation between tracheid properties were much greater on the among-specimens scale than on the within-specimen scale as a function of maturity and growth rate (Table 7). However, statistical significance was more difficult to achieve because of the smaller number of observations.

As a function of increasing cambium maturity, a slightly positive correlation appeared between tracheid length on the one hand, and cross-sectional compactness and solid fraction on the other (Table 7). The positive correlations between tracheid perimeter and tracheid coarseness, length, and cross-sectional cell-wall area became significantly reduced as a function of increasing cambium maturity. Cor-

relations between solid fraction, coarseness, and cell-wall thickness increased correspondingly. The inverse phenomena in the apparent effect of apical maturity already mentioned are again apparent.

The correlation between cross-sectional cell-wall area and tracheid perimeter increased with physiological intensity (Table 7) and the negative correlation between perimeter and compactness also became stronger.

Genotype effects

It is interesting to consider to what degree the variation in tracheid properties may be due to variation in tree genotype. A detailed investigation of this subject would require molecular genetics, which is beyond the scope of this study. However, we are able to compare the variation in tracheid properties within a particular tree in relation to the variation between trees.

First, let us consider the overall magnitude of variation in tracheid properties within a sample tree. The mean values of the coefficients of variation for different tracheid properties for any tree, as well as the standard deviation of these coefficients, are shown in Fig. 3. We find that in relation to the within-tree variation, the magnitude of variation between trees is not dramatic. Trees with fewer than three specimens were disregarded from these and subsequent analysis.

It appears from Fig. 3 that the coefficients of variation of tracheid properties vary between trees somewhat more on the among-specimens scale than on the within-specimen scale. It is instructive to consider whether this also holds for the variation in any particular tracheid property between trees. Fig. 4 confirms this: the magnitude of variation in any tracheid property varies more between trees on the among-specimens scale than on the within-specimen scale. This finding is in line with the results in Table 6b: maturity, and to some degree growth rate, contribute significantly to the magnitude of variation within a tree.

Coefficients of correlation between tracheid

properties within genotypes, i.e. within individual sample trees, are shown in Fig. 5. The within-specimen correlations do not vary significantly from tree to tree. Among-specimens correlations involving cross-sectional geometry on the one hand, and size-scale variables of tracheids on the other, do vary significantly from tree to tree. This finding is in agreement with Table 7, these correlations being strong functions of cambium maturity. There is thus no reason to assume that the variation of genotype between trees would significantly contribute to the variation in tracheid properties within these experimental sample series.

Property combinations of individual tracheids

At least three technical methods are available for classifying tracheids:

1. Wood classification, based on maturity or growth rate
2. Screening of individual tracheids according to a dimension determined by tracheid orientation
3. Hydrodynamic fractionation according to specific surface.

Nothing prevents combining several of these classification methods. Here we will consider combinations of tracheid properties achievable by combining wood classification with either screening or hydrodynamic fractionation.

Let us first discuss the screening option. Where tracheids are oriented parallel to the screen openings, the fractionation occurs mainly according to tracheid length (cf. Tasman 1972; Karnis 1997). Let us apply this kind of screening to tracheid populations classified according to cambium maturity. We see in Fig. 6 that the oblongness of tracheids increases as a function of tracheid length. The cross-sectional cell-wall area of tracheids does increase with tracheid length, but slower than the second power of length, resulting in the increase in oblongness. Tracheids of specified length show no difference in oblongness between cambium maturity classes. This observation is not in disagreement with previous re-

Within   ■ Tree 1   ▲ Tree 2   ● Tree 3   □ Site 1 ■ Site 2 ○ Site 3 ● Site 4   Within
   □ Tree 4   ○ Tree 6
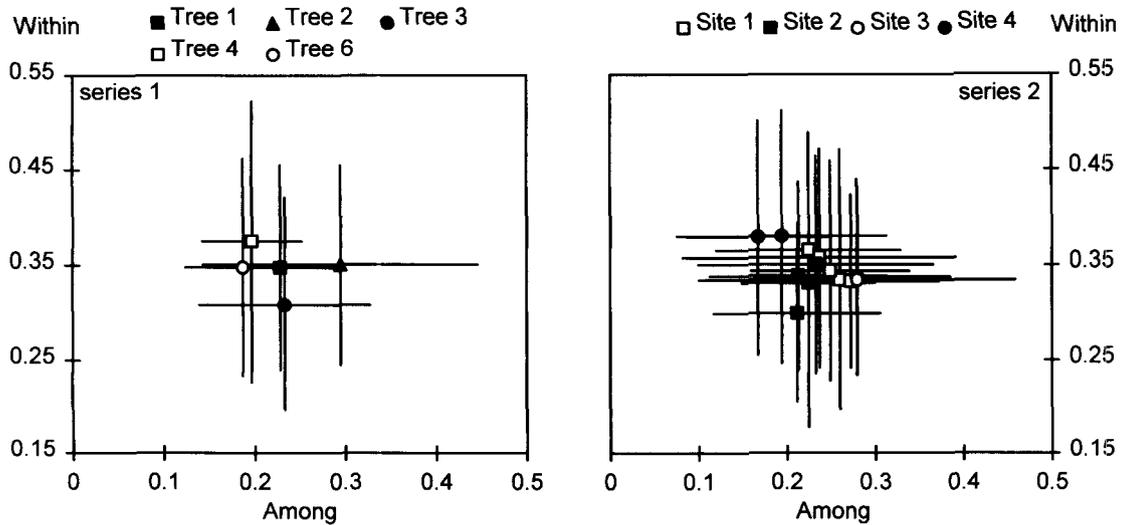
FIG. 3.   Variability of coefficients of variation of tracheid properties within individual sample trees. Error bars indicate the standard deviation.

sults reporting an increasing oblongness as a function of cambium maturity (Sirviö and Kärenlampi 1998); since tracheid length increases with maturity (Hartig 1892, 1898), the oblongness does as well.

We also see in Fig. 6 that the cross-sectional compactness of tracheids does not significantly change with tracheid length. This is because

tracheid perimeter is proportional to tracheid length in a power that approximately equals the square root of the proportionality exponent of cross-sectional cell-wall area.

Combinations of properties of tracheids screened according to tracheid length, but classified according to physiological intensity (the dimensionless, maturity-independent measure

Within   ■ Length ▲ Area ● Perimeter   □ Thickness ▲ Oblongness ○ Compactness   Within
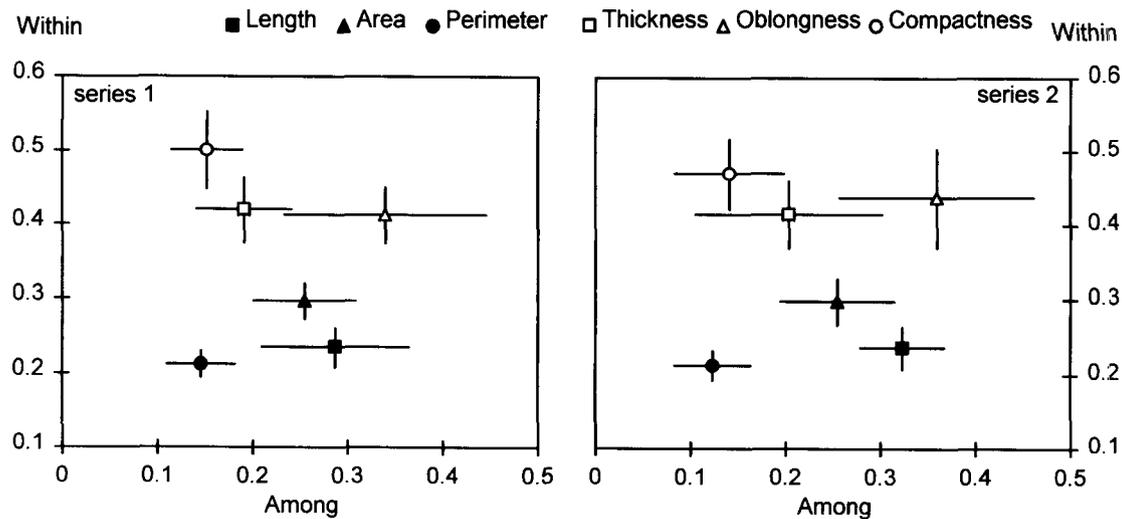
FIG. 4.   Variability of coefficients of variation of tracheid properties between trees. Error bars indicate the standard deviation.
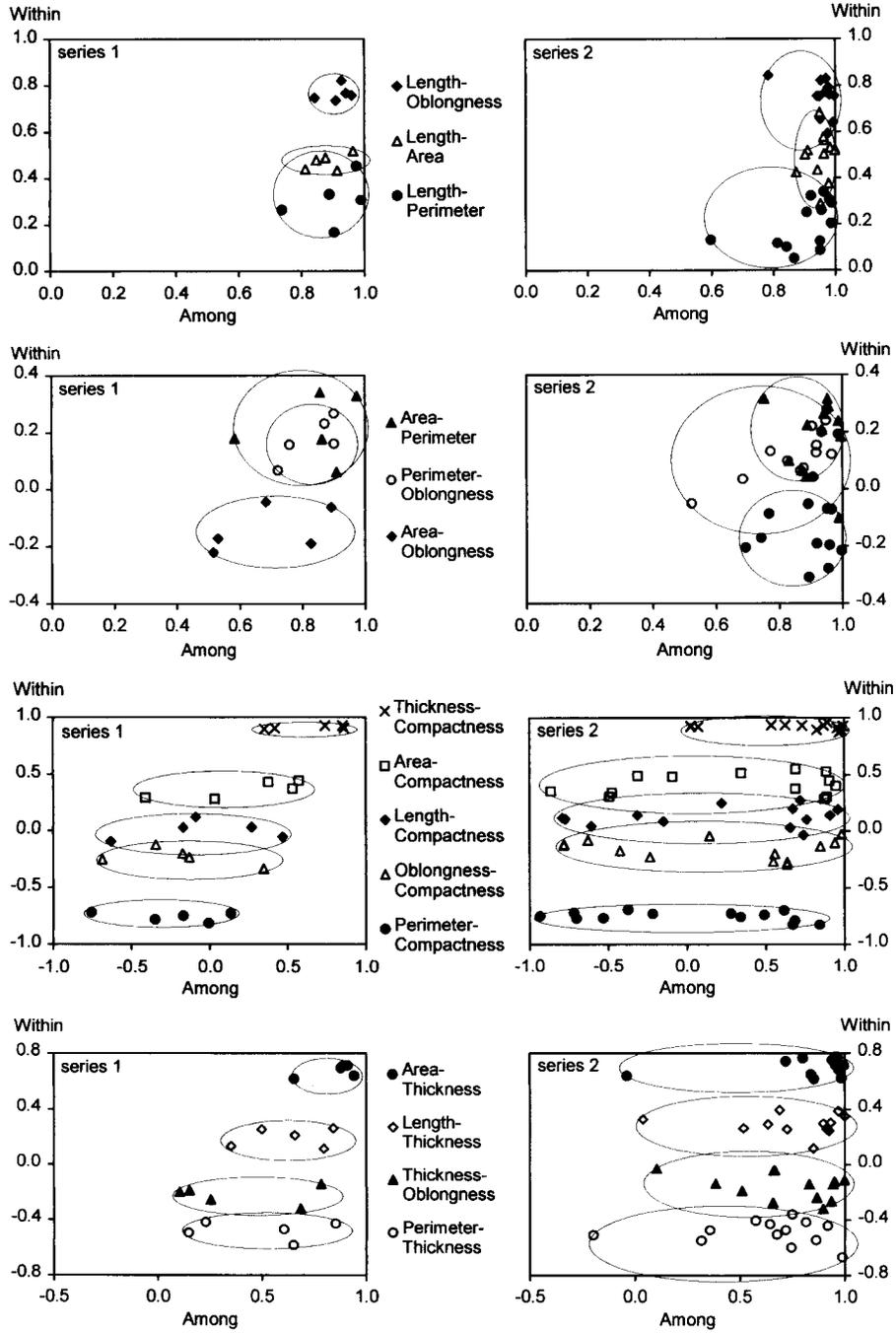
FIG. 5.   Coefficients of correlation between tracheid properties within individual sample trees.
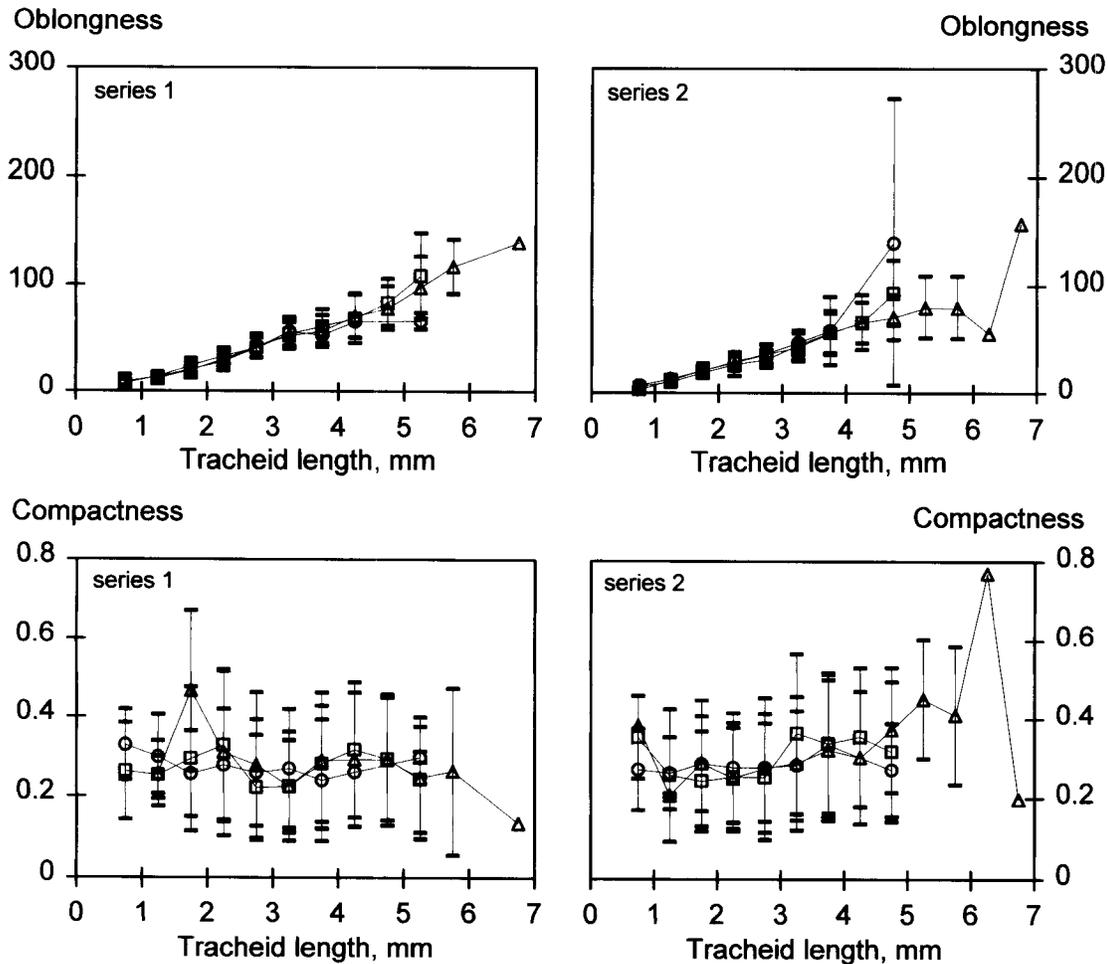
FIG. 6. Oblongness and compactness of tracheids of different length classes in tracheid populations classified according to cambium maturity (circle = low, square = medium, triangle = high). Error bars indicate the standard deviation.

of growth rate), are shown in Fig. 7. We find that the relationship between the oblongness and the tracheid length within and between these classes is similar to the case of maturity classes (cf. Fig. 6). The compactness of tracheids within a growth-rate class is not a strong function of tracheid length. However, the higher the growth rate, the lower the compactness at a specified length. This arises from the heavy dependence of compactness on the growth rate (Sirviö and Kärenlampi 1998).

Let us then consider screening where tracheids are oriented perpendicular to the screen

openings (Ora et al. 1993). Now, the fractionation occurs mainly according to tracheid width, which is represented by perimeter in our data. We find in Fig. 8 that at a specified perimeter class, both oblongness and compactness are greater, the greater the cambium maturity. Regarding oblongness, the reason is that the second power of length at a specified perimeter class is a stronger function of maturity than the cross-sectional cell-wall area is, even though both increase with maturity. A natural consequence of the latter is that the higher the maturity, the higher the compact-
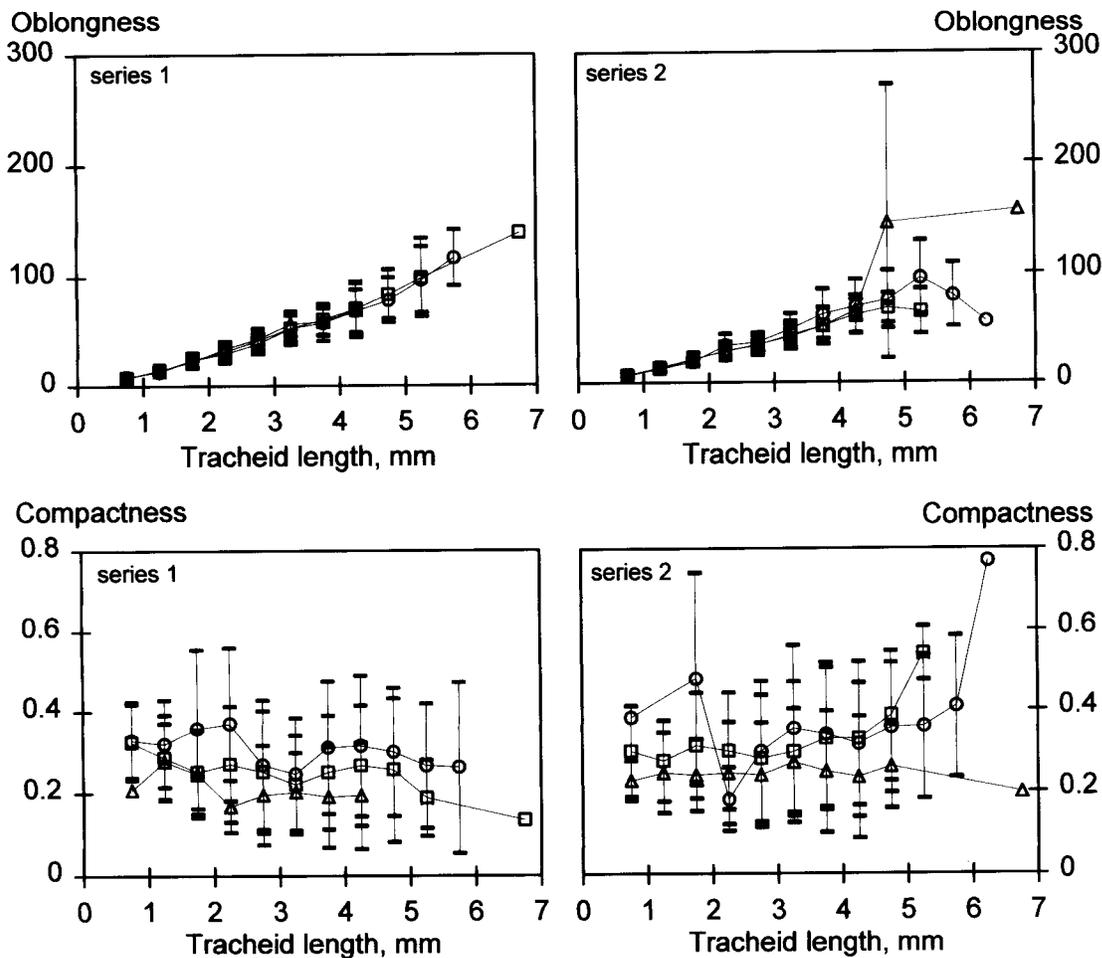
FIG. 7. Oblongness and compactness of tracheids of different length classes in tracheid populations classified according to growth rate (circle = low, square = medium, triangle = high). Error bars indicate the standard deviation.

ness at a specified perimeter. In each maturity class, tracheid compactness clearly decreases with increasing perimeter (Fig. 8).

Tracheid populations classified according to growth rate prior to screening with respect to width also demonstrate a significantly decreasing compactness as a function of perimeter (Fig. 9). The higher the growth rate is, the lower the compactness at any perimeter class is because of the thinner cell-walls (Sirviö and Kärenlampi 1998). At a specified perimeter class, the oblongness is smaller with a higher growth rate. Both tracheid length and cross-sectional cell-wall area decrease with increas-

ing growth rate, but the square of tracheid length decreases faster than the cross-sectional cell-wall area. Within a growth-rate class the oblongness increases only slightly with perimeter, because the increment in tracheid length and cross-sectional cell-wall area as a function of perimeter are of the same magnitude.

Let us now discuss hydrodynamic fractionation according to specific surface (cf. Karnis 1997). Tracheids being long, their specific surface is determined by cross-sectional dimensions, and can be conveniently approximated as the ratio of perimeter to cross-sectional cell-wall area. We find in Fig. 10 that at a specified
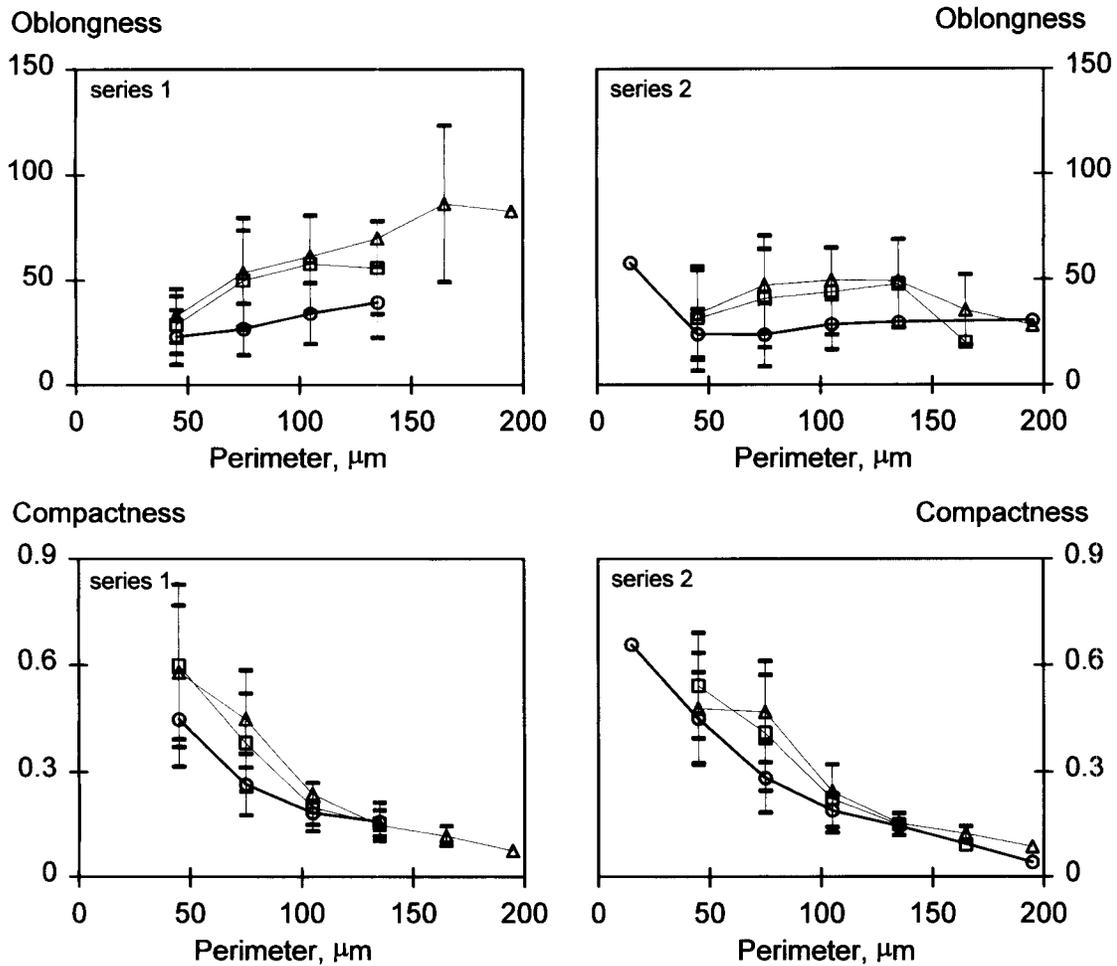
Fig. 8. Oblongness and compactness of tracheids of different perimeter classes in tracheid populations classified according to cambium maturity (circle = low, square = medium, triangle = high). Error bars indicate the standard deviation.

specific surface, the oblongness of tracheids produced by high-maturity cambium is higher because of greater tracheid length at a specified specific surface. We also find that the compactness of tracheids of a specified cambium maturity class considerably decreases with specific surface. Compactness at a specified specific surface is the lower the higher the cambium maturity. The latter is a pure size-scale effect, since for objects of specified geometry, specific surface decreases with size.

Tracheid populations classified according to growth rate prior to fractionation with re-

spect to specific surface also demonstrate a significantly decreasing compactness as a function of specific surface (Fig. 11). This is natural, because if the perimeter is kept constant, the cross-sectional cell-wall area has to be decreased in order to increase the specific surface, which then shows as a decrease in compactness. At a specified specific surface, the different growth rate classes do not differ in compactness. It is, however, worth noting that on the average, compactness is higher with a lower growth rate (Sirviö and Kärenlampi 1998). Thus, on the average, the lower
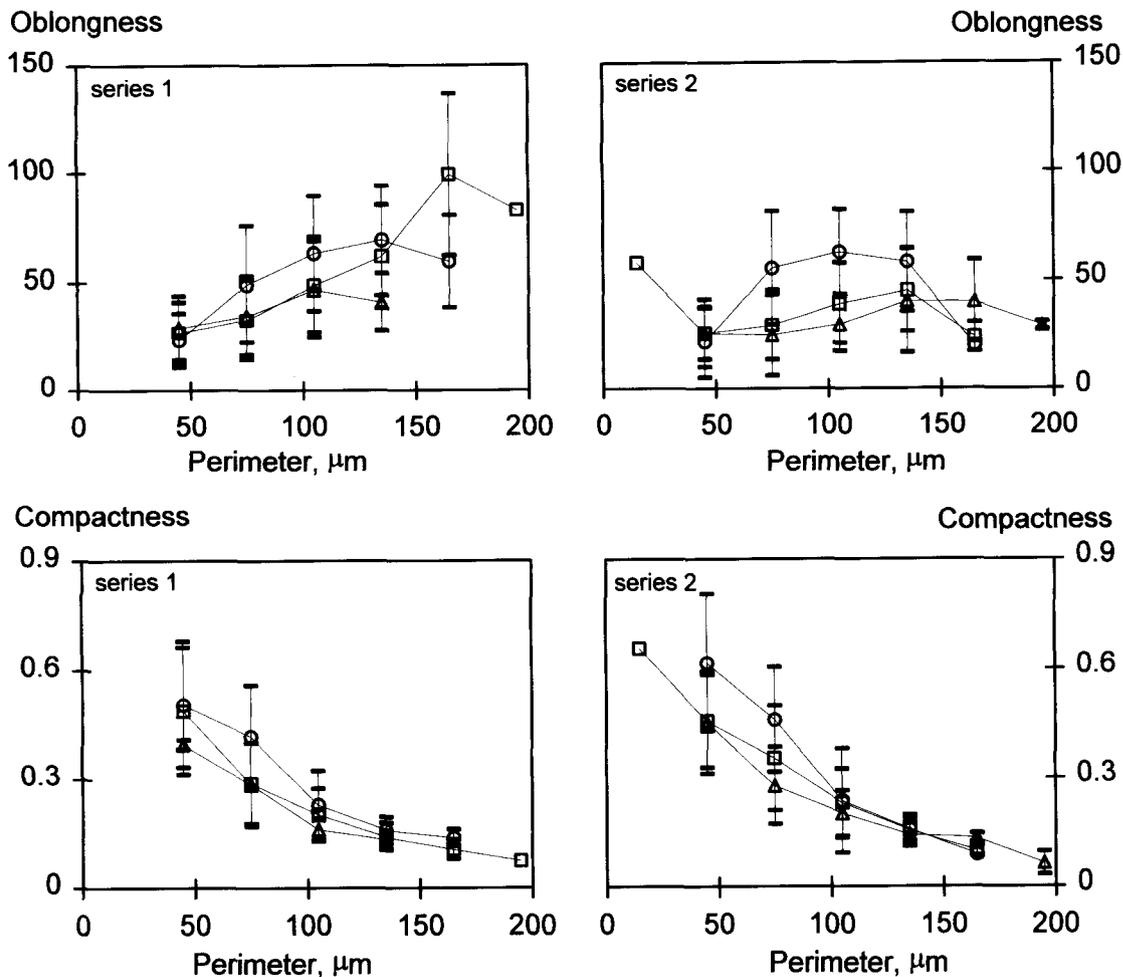
FIG. 9.   Oblongness and compactness of tracheids of different perimeter classes in tracheid populations classified according to growth rate (circle = low, square = medium, triangle = high). Error bars indicate the standard deviation.

the growth rate, the lower the specific surface. Oblongness, however, is highest within the low-growth-rate class because of longer tracheids. At a specified growth-rate class, the oblongness does not change significantly as a function of specific surface. Tracheids with high specific surface are smaller. The square of tracheid length and the cross-sectional cell-wall area decrease roughly in proportion. However, the perimeter is almost invariant, the decrement of the cross-sectional cell-wall area being due to decrement in cell-wall thickness.

CONCLUSIONS

Within-specimen variation dominates the overall variability within a genotype, an exception being the variation in tracheid length, which is stronger among specimens.

The magnitude of variation in tracheid properties is a strong function of cambium maturity. Variation in properties mainly depending on cambium maturity is significantly reduced by classifying wood according to maturity. This particularly applies to the size-scale variables of tracheids, as well as tracheid oblongness (cf. Sanio 1872; Hartig 1892,
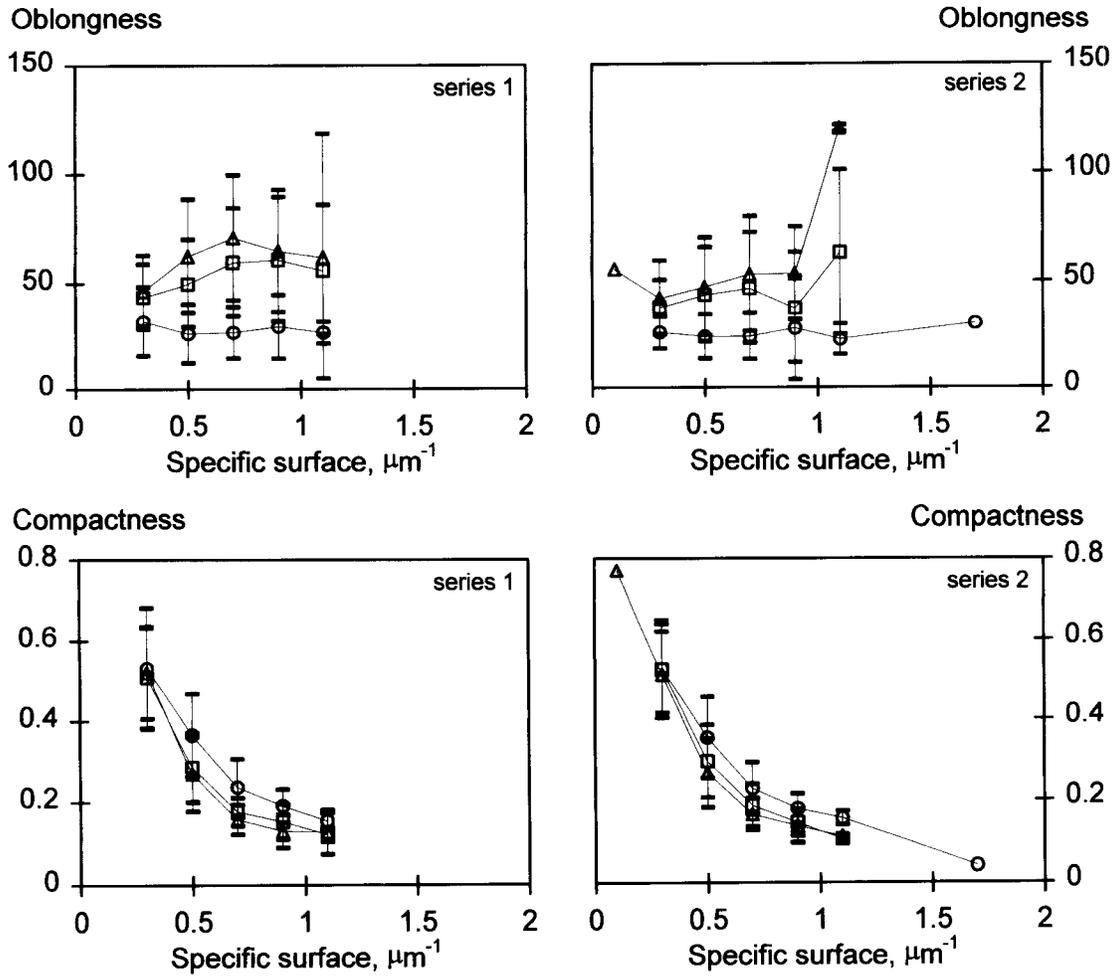
Fig. 10. Oblongness and compactness of tracheids of different specific-surface classes in tracheid populations classified according to cambium maturity (circle = low, square = medium, triangle = high). Error bars indicate the standard deviation.

1898, 1901; Mork 1928; Atmer and Thörnqvist 1982; Sirviö and Kärenlampi 1998). Maturity classification particularly reduces the among-specimen variation (Table 6b, Fig. 4).

Interrelationships between tracheid properties also are strong functions of cambium maturity, particularly those involving both size-scale variables and cross-sectional geometry (Table 7, Fig. 5).

Combinations of tracheid properties, achievable using different screening and fractionation techniques, depend on the wood classification procedure used. Apart from

wood classification, tracheid oblongness can be controlled by screening with respect to tracheid length. Tracheid compactness can be effectively controlled by hydrodynamic fractionation.

Results shown by the two independent sample series, collected using different procedures, appear to be even surprisingly consistent. This indicates that the phenomena investigated are characteristic of Norway spruce, instead of being peculiar to the trees or stands sampled. These results may be applicable to other *Picea* species; other conifers
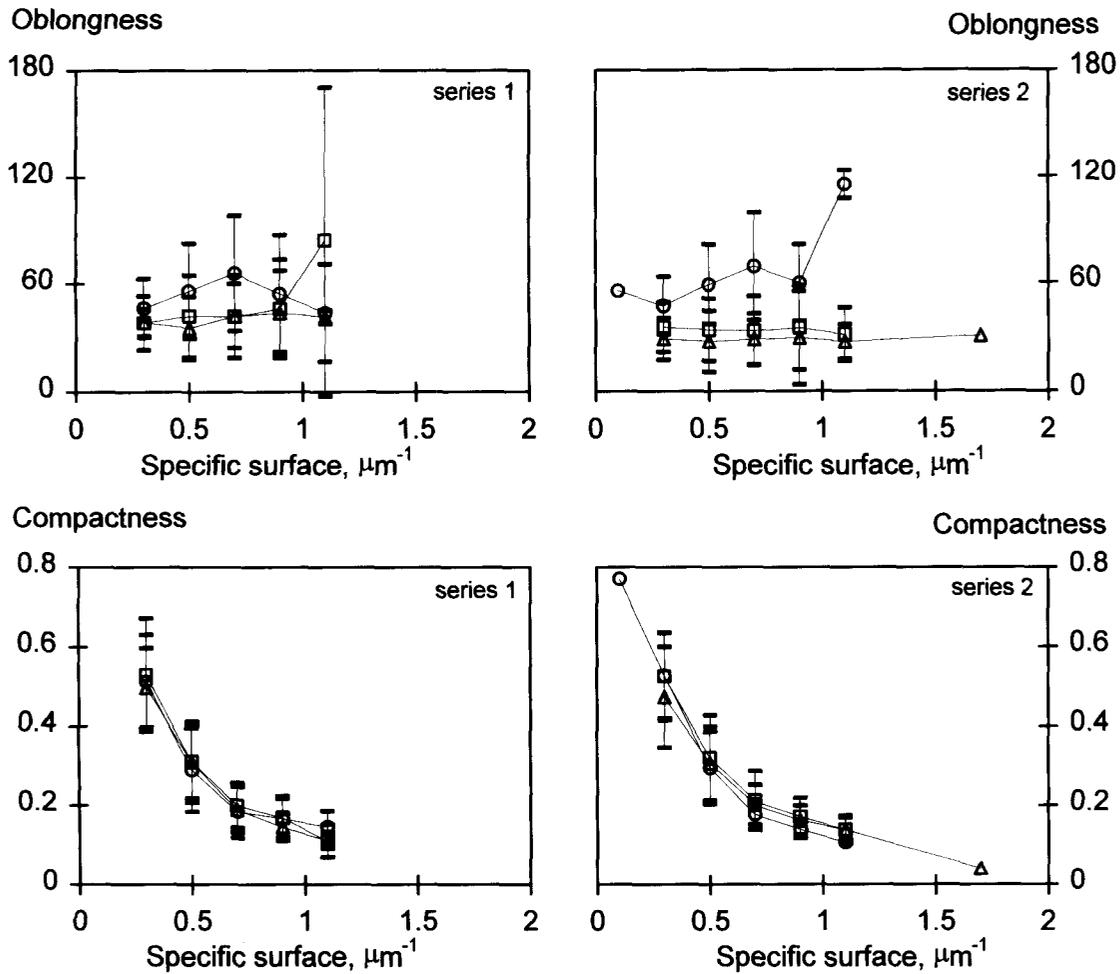
Fig. 11. Oblongness and compactness of tracheids of different specific-surface classes in tracheid populations classified according to growth rate (circle = low, square = medium, triangle = high). Error bars indicate the standard deviation.

will probably require investigations of their own.

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