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Wood Density within Norway Spruce Stems

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We studied the variation in average wood density of annual rings, earlywood density, and latewood density in addition to ring width and latewood percentage within Norway spruce (*Picea abies* (L.) Karst.) stems from the pith to the bark, and from the stem base towards the stem apex. Moreover, the variation in wood density within annual rings was studied at the different heights and radial positions in the stem. The material consisted of 85 trees from central and south-eastern Finland. Variation between the annual rings accounted for 11–27% of the total variation in wood density. Only small differences (3–6%) in wood density were found between different heights in the stem. The largest (49–80%) variation in wood density was found within the annual rings. The difference in wood density between earlywood and latewood was smaller in the rings near the pith than in the outer rings. The increasing wood density from the pith outwards was related to increasing latewood density and latewood percentage, whereas the earlywood density increased only slightly from the pith outwards. In a given cambial age (i.e., given rings from the pith), the average wood density of annual rings increased with increasing stem height. In contrast, in the rings formed in the same calendar years (i.e., given rings from the bark), the average wood density of annual rings decreased with increasing stem height. The results of this study verify our knowledge of wood density variation and can further contribute to creating models to predict wood density.

Keywords inter-ring variation, intra-ring variation, maturation, *Picea abies*, wood density
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1 Introduction

In the Nordic countries, Norway spruce (*Picea abies* (L.) Karst.) is a tree species with high ecological and industrial importance. Wood properties determine the end-product quality in industrial processes. Wood density (WD) is a commonly used indicator of wood quality since it is related to tracheid properties, pulp yield and timber strength. Efforts to improve wood properties are only worthwhile if the wood structure and its natural variation are known in detail.

The within-tree variation of WD can be divided into radial variation from the pith to the cambium, axial variation from the stem base to the stem apex, and intra-ring variation (e.g., Panshin and de Zeeuw 1980). The radial variation in average WD of individual annual rings in Norway spruce is well-known (Olesen 1977, Frimpong-Mensah 1987, Petty et al. 1990, Danborg 1994, Saranpää 1994, 2003). WD decreases from the pith outwards until the minimum value is reached around rings 10–20 (Danborg 1994, Saranpää 1994). Thereafter in mature wood, WD again increases with the increasing cambial age, i.e., the increasing ring number from the pith to the bark (Olesen 1977, Frimpong-Mensah 1987, Petty et al. 1990, Jaakkola et al. 2005a).

As compared to radial variation, the axial variation in WD of Norway spruce has been less extensively studied. Three different approaches can be applied while studying the axial variation in WD: 1) in given annual rings counted from the pith to the bark, i.e., with increasing cambial age; 2) in given annual rings counted from the bark towards the pith; and 3) from stem cross-sectional discs. Some studies have reported a general increase in WD of Norway spruce from the stem base towards the tree top while measured at the same distance or at the same ring number from the pith (approach no. 1; Frimbong-Mensah 1987, Petty et al. 1990, Saranpää 2003, Molteberg and Høibø 2006). However, these studies presented no data on the intra-ring variation in WD between different heights and radial positions in the stem. Moreover, most of the existing studies on the axial variation in WD of Norway spruce have been based on the mean WD of cross-sectional discs (approach no. 3), and the results have been contradictory showing either increasing or decreasing WD along the stem (see e.g., Hakkila 1966, Hakkila and Uusvaara 1968, Olesen 1982, Atmer and Thörnqvist 1982, Frimbong-Mensah 1987, Johansson 1993, Repola 2006).

The intra-ring variation of WD is large, shifting from ca. 300 kg m^{-3} in earlywood to ca. 1000 kg m^{-3} in latewood (Olesen 1982, Mäkinen et al. 2002b, Decoux et al. 2004). The increase in WD from early- to latewood is mainly due to anatomical changes in tracheids (Kellogg and Wangaard 1969, Skaar 1988). However, studies of high resolution on the intra-ring variation of WD from the pith to the bark at the different heights in the Norway spruce stem are scarce.

In this study, we analysed in detail the variation in average WD of individual annual rings (RD), earlywood density (ED), latewood density (LD), ring width (RW) and latewood percentage (LW%) from the stem base to the stem apex with the given radial positions in the stem. Moreover, we studied the variation in WD within annual rings from the stem base to the stem apex with the given radial positions in the stem. Since the tree growth is negatively related with the WD of Norway spruce, as shown by numerous researchers (e.g., Hakkila 1966, Hakkila and Uusvaara 1968, Olesen 1976, 1977, Petty et al. 1990, Danborg 1994, Lindström 1996, Dutilleul et al. 1998, Herman et al. 1998a, Pape 1999, Mäkinen et al. 2002b, Wilhelmsson et al. 2002, Saranpää 2003), we also analysed the variation in WD of Norway spruce independent of the effects of growth rate, i.e., annual ring width. This approach allowed us to determine the amount of variation explained by factors other than growth rate (i.e., cambial age, height in the stem, inter-tree variation) contributing to WD variation within Norway spruce stems.

Abbreviations

WD, wood density; RD, average wood density of individual annual rings (g cm^{-3}); ED, average earlywood density (g cm^{-3}); LD, average latewood density (g cm^{-3}); RW, annual ring width (mm); LW%, latewood percentage (%); TH, relative tree height (%); Cambial age-class, group of given annual rings counted from the pith to the bark; Ontogenic age-class, group of given annual rings counted from the bark to the pith.

Table 1. Characteristics of the experiments in Parikkala (Pa) and Suonenjoki (Su).

Site	Location	Altitude a.s.l. (m)[a]	Temp. sum (d.d)[b]	Site index H_{100} (m)[c]	AVI ($m^3ha^{-1}a^{-1}$)[d]	Stand age yrs (in 2002)	No. trees	Height H_{dom} (m)[e]	DBH (cm)[f]	Crown ratio[g]
Pa	61°36’N 29°22’E	99	1211	28.5	12.2	63	45	22.7	24.9	0.61
Su	62°45’N 27°00’E	154	1118	28.8	14.9	76	40	26.1	27.9	0.55

[a]Above sea level.
[b]Degree-days (Ojansuu and Henttonen 1983).
[c]Dominant height at the age of 100 years (Gustavsen 1980; Vuokila and Väliaho 1980).
[d]Annual volume increment during the experiment; in Pa 1977–2002 and in Su 1978–2003.
[e]Dominant height of the 100 thickest trees per ha.
[f]Diameter at breast height (1.3 m) of the sample trees.
[g]Crown length (dm) of sample trees divided by tree height (dm).

The material of this study (85 stems) was previously analysed for the effects of long-term fertilisation and thinning treatments on radial growth rate, WD (Jaakkola et al. 2006), as well as tracheid properties and lignin content (Jaakkola et al. 2007). The experimental design comprised three fertilisation and three thinning treatments of varying timing and intensity, giving rise to nine different combinations of treatments in two experiments. The results showed that normal (T_1) and intensive first thinning (T_2) increased the radial growth rate of the trees by 8% and 29% as compared to delayed first thinning (T_0); at the same time no essential changes in WD, tracheid properties or lignin content were detected. Fertilisation (F_1 and F_2) enhanced radial growth rate by about 40% as compared to the unfertilised control, while the corresponding decrease in WD was 7% and no essential changes in tracheid properties and lignin content were found.

Primarily, this study aims to verify our knowledge of the inter- and intra-ring variation in WD of Norway spruce from the stem base to the stem apex and from the pith to the bark. Secondly, the results of this study contribute to creating more accurate models for predicting WD in individual annual rings of Norway spruce (see Mäkinen et al. 2007).

2 Materials and Methods

2.1 Sample Trees

The material of this study was collected from two fertilisation-thinning experiments in Parikkala and Suonenjoki located in south-eastern and central Finland (Table 1). Stands were planted in 1939 in Parikkala, and in 1925 in Suonenjoki. They were even-aged and almost entirely Norway spruce. They were located on mineral soil classified as *Oxalis-Myrtillus* forest site type (OMT) corresponding to highly fertile sites typical for Norway spruce (Cajander 1949). The fertilisation-thinning experiments were established in 1977 in Parikkala and in 1978 in Suonenjoki. Both experiments included three thinning and three fertilisation treatments in a randomised block design, with each treatment combination occurring only once. Thus, the total number of plots, i.e., treatment combinations, was nine in both experiments. Fertilisation treatments were: unfertilised (F_0); 150 kg nitrogen (N), 75 kg phosphorus oxide (P_2O_5) and 75 kg potassium oxide (K_2O) per ha (F_1); and 300 kg (N), 150 kg (P_2O_5) and 150 kg (K_2O) per ha (F_2). On the fertilised plots, NPK fertiliser was applied at 5-year intervals. The thinning treatments were: delayed first thinning, i.e., ca. 60% of the original number of stems removed 15 years after establishment (T_0); normal thinning, i.e., about 30% of the original number of stems removed at establishment, and ca. 30% of the original number of stems 10 years after establishment (T_1), and intensive first thinning with about 60% of the original number of stems removed at the establishment of the experiment

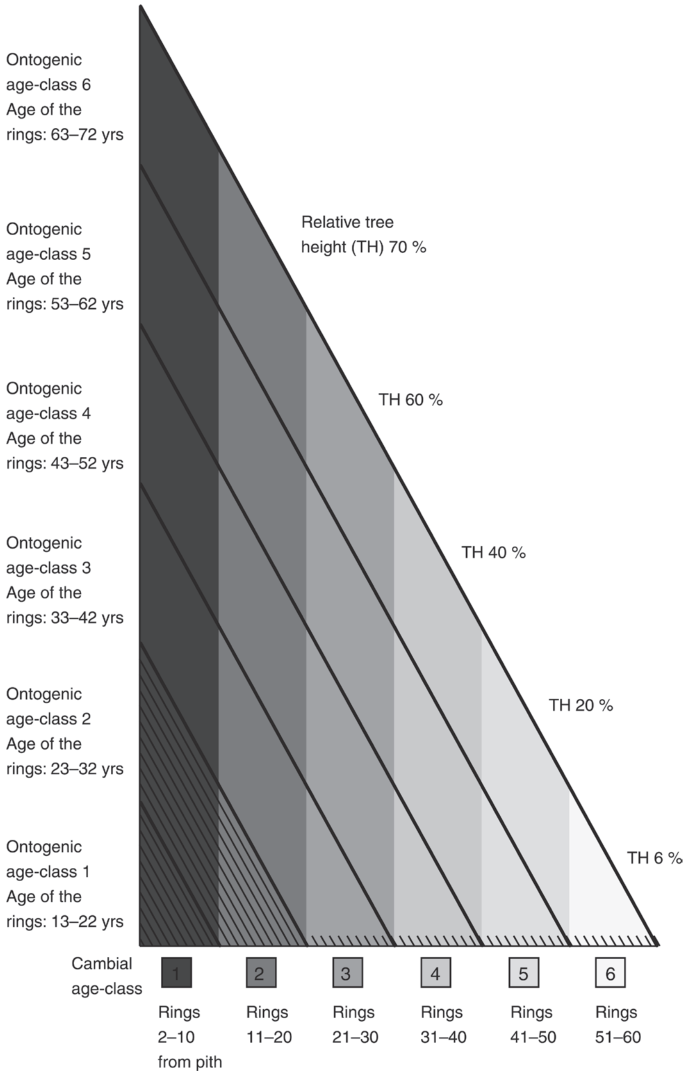

Fig. 1. Schematic presentation showing the grouping of the annual rings into different cambial age-classes and ontogenic age-classes at different relative heights in the tree. Redrawn and modified from Duff and Nolan (1953) and Schweingruber et al. (2006). Note: the annual rings in the cambial and ontogenic age-classes of the same number are not necessary identical.

(T_2). The plots were thinned from below. For more information on the treatments, see Jaakkola et al. 2006, 2007.

Altogether 85 sample trees were harvested from Parikkala and Suonenjoki experiments. In both experiments on each plot, the cumulative basal area distribution was divided into five classes of equal basal area. One sample tree was randomly harvested per each size class on each plot. In Suonenjoki, however, plot F_2T_0 was excluded because it had been damaged by wind. Thus, altogether 40 sample trees were harvested in Suonenjoki and 45 trees in Parikkala.

One sample disc was taken at breast height (1.3 m), avoiding whorls and defects, from all the sampled trees grown in all the different plots (F_0T_0, F_0T_1, F_0T_2, F_1T_0, F_1T_1, F_1T_2, F_2T_0 (except in Suonenjoki), F_2T_1, and F_2T_2) in both sites. Moreover, from the trees grown on the plots F_0T_0, F_0T_1, F_0T_2, F_1T_0, F_1T_1, and F_1T_2 in both sites, additional sample discs were taken at 4-metre intervals above breast height (i.e., 5 m, 9 m, etc.) until the stem diameter was less than 16 cm, and thereafter at 3-metre intervals until the stem diameter fell below 8 cm. The sampling heights were further converted into relative heights in the trees (TH; % = height of sample disc / tree height × 100%). Since the relative heights varied between individual trees, they were further grouped into five classes of equal length along the stem (TH 6%, 0–16% of stem height; TH 20%, 17–32%; TH 40%, 33–48%; TH 60%, 49–64%; TH 70%, 65–80%; Fig. 1).

2.2 Measurements of Wood Density

For the measurements of WD, annual ring width (RW) and latewood percentage (LW%), 8 cm thick wedges were sawn from the sample discs. The wedges were air-dried for six months, and samples (5 mm × 5 mm) were sawn throughout the south radius. Since Norway spruce wood contains only ca. 1% resins (Ekman 1980, Holmbom et al. 1991), no extractions were performed. The moisture content was adjusted to 12% by keeping the samples at 20°C and a relative humidity of 65% for three weeks. The samples were then placed on a film and X-rayed for 5 min, 16 kV, 20 mA, at a distance of 2.5 m (Saikku 1975, Jaakkola et al. 2006). Films were scanned, and a continuous wood-density profile (i.e., weight density, 12% moisture content, g cm^{-3}) for each sample was measured using WinDendro™ software (version 6.4, Regent Instruments Inc., Québec, Québec, Canada). The resolution of the captured images was 25.4 μm pixel^{-1} (256 grey levels). In addition, RW and LW% were determined for each annual ring. For each annual ring, a transition point (TP) between earlywood and latewood was separately defined as follows:

$$TP_{thr} = MAX_{thr} - (MAX_{thr} - MIN_{thr}) \times 0.3 \qquad (1)$$

where MAX_{thr} and MIN_{thr} are the maximum and minimum WD of the annual ring r, at height h, and on tree t, respectively. When TP were examined visually, the factor 0.3 was found to have the best fit to the captured images.

The radial position in the stem was determined both as (1) a cambial age, i.e., ring number counted from the pith to the bark, meaning that the given ring from the pith had the same cambial age, but at the various heights in the stem the rings were formed during various years; and as a (2) ring number counted from the bark to the pith, meaning that at the various heights the given ring from the bark was formed in the same calendar year. Since the trees from different sites had a different number of annual rings at the selected heights, the ontogenetic age was determined for rings counted from the bark, i.e., the difference between the calendar year when the ring was formed and the year when the tree was born (Schweingruber et al. 2006). This approach enables the within- and between-stem analysis of WD, considering both the differences in tree age between stems, and the same growth conditions of the given annual ring counted from the bark to the pith at various heights in each tree.

The annual rings were grouped into classes according to the cambial age, i.e., cambial age-classes 1–6 (cambial age-class 1, rings 2–10 from the pith,…, cambial age-class 6, rings 51–60 from the pith; Fig. 1 and Table 2), and the ontogenetic age, i.e., ontogenetic age-classes 1–6 (ontoge-

Table 2. Grouping of annual rings into different cambial and ontogenic age-classes.

Cambial age-class	Cambial age of rings [a]
1	2–10
2	11–20
3	21–30
4	31–40
5	41–50
6	51–60
Ontogenic age-class	**Ontogenic age of rings [b]**
1	13–22 [c]
2	23–32
3	33–42
4	43–52
5	53–62
6	63–72 [d]

[a] annual ring number from the pith; [b] difference between the calendar year of ring formation and calendar year of tree born, i.e., the annual rings near the pith at the stem base are ontogenetically youngest and those near the bark are ontogenetically oldest, and all the rings of ontogenetically same age at various heights in each tree were formed during the same calendar years; [c] Ontogenic age-class 1 only in Parikkala; [d] Ontogenic age-class 6 only in Suonenjoki. Note: the annual rings in the cambial and ontogenic age-classes of the same number are not necessary identical.

netic age-class 1, the age of the rings 13–22 yrs,…, ontogenetic age-class 6, the age of the rings 63–72 yrs; Fig. 1 and Table 2). Each class of cambial age and ontogenetic age per tree consisted of 10 rings (with exception of 9 rings in cambial age-class 1). The total number of rings per each cambial and ontogenetic age-class was 100–850, depending on TH. An arithmetic mean of the individual pixel densities for RD, ED, LD was determined for each individual annual ring and for each cambial and ontogenic age-class at the various TH. Moreover, the average RW and LW% were determined for cambial and ontogenic age-classes at the various TH.

Additionally, in order to examine the variation in WD within individual annual rings, the relative position of each measured pixel within an annual ring was determined and each ring was divided into ten parts of equal size.

2.3 Statistical Analyses

Mixed model analysis was carried out to study the variation in WD explained by the tree, TH, and radial position in the tree (for the determinations of the radial position, see above). The whole data set, i.e., the WD of each individual pixel (p) (excluding the first annual ring counted both from the pith and from the bark) was used as a dependent variable. The data was not normally distributed and, therefore, earlywood and latewood were analysed separately. Moreover, a logarithmic transformation was used for both ED and LD. The observations in the data have a hierarchical structure (tree, TH, annual ring at the given height, individual pixel within an annual ring). In the mixed models, this correlation structure of dependent variables was taken into account by using random variables describing the nested effects of trees, TH and radial positions in the trees.

In this study, we wanted to analyse factors other than radial growth rate that affect WD. For that purpose, RW of each annual ring was used as a covariate (RW_{thr} in Eq. 2) in order to remove the effect of growth rate on WD. The log-transformed WD of individual pixels was linearly related to the covariate.

To analyse the variation in WD between the trees, TH and annual rings, and within annual rings, a nested model for hierarchical data structure was used:

$$\log(y_{thrp}) = \mu + \beta RW_{thr} u_t + u_{th} + u_{thr} + \varepsilon_{thrp} \quad (2)$$

where y_{thrp} is the dependent variable; μ the general mean; β the regression coefficient for covariate RW_{thr}, i.e., ring width of each annual ring (fixed effect in the model); u_t the random effect of the tree t; u_{th} the random effect of relative height h within the tree t; u_{thr} the random effect of annual ring r (i.e., cambial age or ontogenic age of an annual ring) within the relative height h and tree t; and ε_{thrp} is the random error. The MIXED procedure of SAS software (SAS 2004; SAS Institute, Inc. Cary, NC, USA) with the estimation of the restricted maximum likelihood (REML) was used in the analysis.

Pearson's simple correlation coefficients (r) between RD, ED, LD, RW and LW% were calculated for each TH, cambial and ontogenic age-class in the stem using the arithmetic mean values of each individual annual ring. Partial correlations (r_p) were calculated for RD and RW in order to

Table 3. Wood density in Parikkala and Suonenjoki: percentage of the variation in earlywood and latewood accounted for by the random variables in Eq. 2.

Parameter	Cambial age % variation	Ontogenic age % variation
$Density_{early}$		
Tree	5.45	5.44
Relative height (within tree)	3.44	4.17
Cambial age (within height & tree)	11.43	–
Ontogenic age (within height & tree)	–	26.98
Residual	79.68	63.40
$Density_{late}$		
Tree	11.13	20.59
Relative height (within tree)	5.87	5.93
Cambial age (within height & tree)	16.15	–
Ontogenic age (within height & tree)	–	24.55
Residual	66.86	48.93

The effect of covariate RW_{thr}, i.e., annual ring width, on WD was significant ($P < 0.001$) both in the analyses of earlywood and latewood density; –, not analysed; for explanation of cambial and ontogenic age, see Table 2.

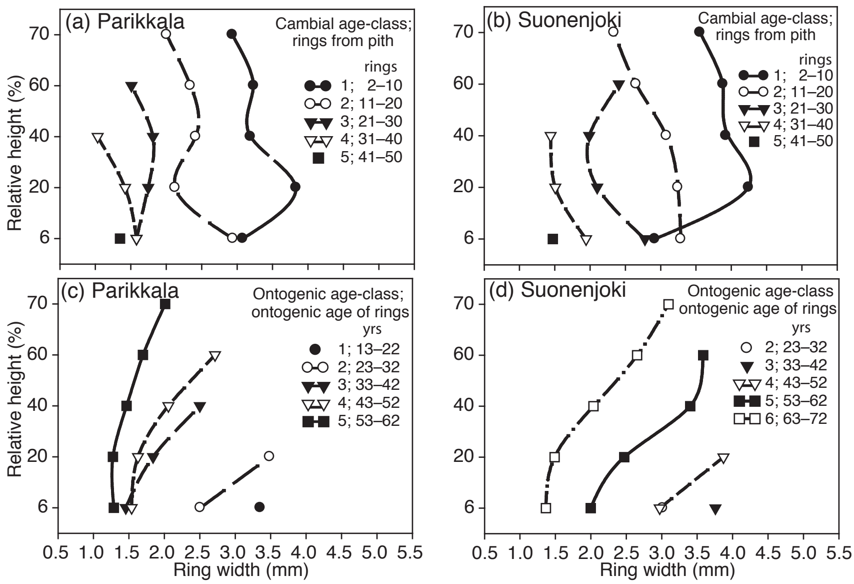

Fig. 2. Ring width along the stem in different cambial (a, b) and ontogenic age-classes (c, d) in Parikkala (a, c) and Suonenjoki (b, d) (for an explanation of cambial and ontogenic age-classes, see Fig. 1 and Table 2).

find out the part of the correlation between them that is not due to their relationship between the third variable, latewood percentage (LW%). The significance levels of the multiple correlations were corrected using Hochberg's step-up adjustment procedure (Hochberg 1988).

3 Results

According to Eq. 2, 5–21% of the variation in ED and LD was between-tree variation (Table 3). Between-ring variation accounted for a somewhat larger part (11–27%) of the variation in WD (Table 3). In contrast, TH accounted for only 3–6% of the variation in WD. The major source of the variation was the within-ring variation (i.e., the residuals of the Eq. 2). It accounted for 63–80% of the variation in ED and 49–67% of that in LD (Table 3). In Figs. 2–7, the variation in RW, LW%, RD, ED and LD is based on the measured data, not on the values predicted by Eq. 2.

3.1 Inter-Ring Variation of Ring Width and Latewood Percentage

At all TH, RW decreased and LW% increased from the pith to the bark (Figs. 2 and 3). In a given cambial age-class, RW decreased and LW% increased with increasing TH (Figs. 2 and 3). In contrast in a given ontogenic age-class, RW increased and LW% decreased with increasing TH (Figs. 2 and 3).

3.2 Inter-Ring Variation of Wood Density

At all TH, RD and LD increased from the pith to the bark (Figs. 4 and 6). In contrast, ED was higher near the pith (in cambial age-class 1, rings 2–10 from the pith), but decreased outwards until the cambial age-class 2 (rings 11–20 from the pith) at all TH (Fig. 5). Thereafter, ED was almost constant or increased slightly with increasing distance from the pith at all TH (Fig. 5).

In a given cambial age-class, RD, ED and LD tended to increase with increasing TH (Figs. 4, 5 and 6). In contrast, in a given ontogenic age-class,

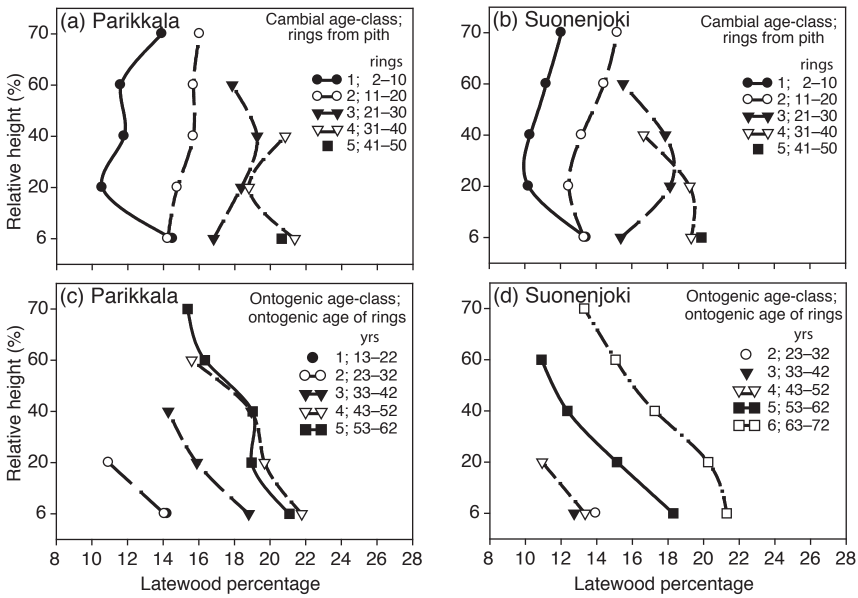

Fig. 3. Latewood percentage along the stem in different cambial age (a, b) and ontogenic age-classes (c, d) in Parikkala (a, c) and Suonenjoki (b, d) (for an explanation of cambial and ontogenic age-classes, see Fig. 1 and Table 2).

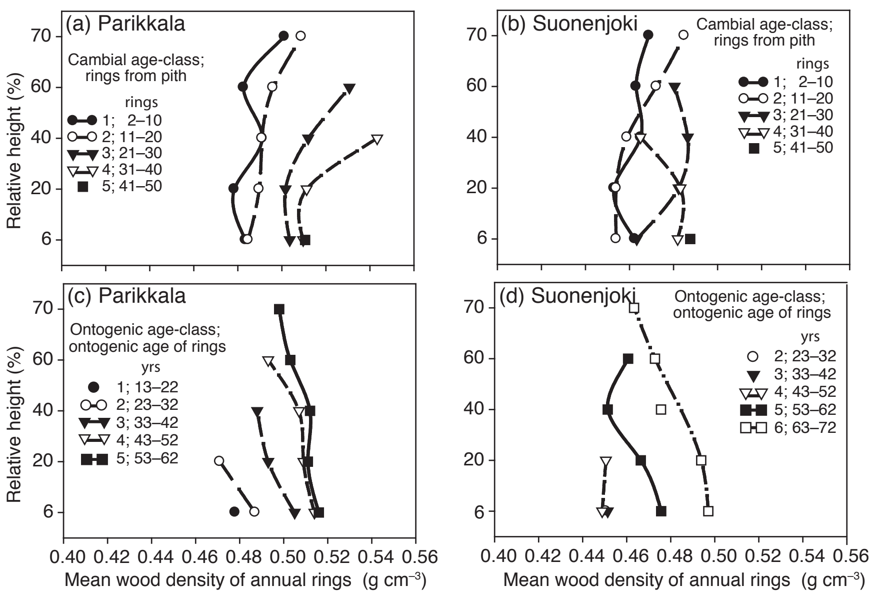

Fig. 4. Mean wood density of individual annual rings along the stem in different cambial (a, b) and ontogenic age-classes (c, d) in Parikkala (a, c) and Suonenjoki (b, d) (for an explanation of cambial and ontogenic age-classes, see Fig. 1 and Table 2).

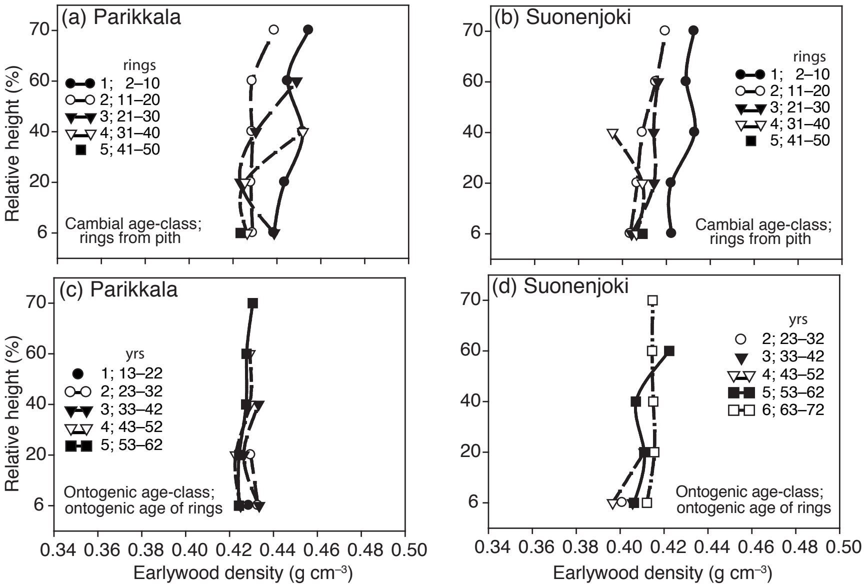

Fig. 5. Earlywood density along the stem in different cambial (a, b) and ontogenic age-classes (c, d) in Parikkala (a, c) and Suonenjoki (b, d) (for an explanation of cambial and ontogenic age-classes, see Fig. 1 and Table 2).

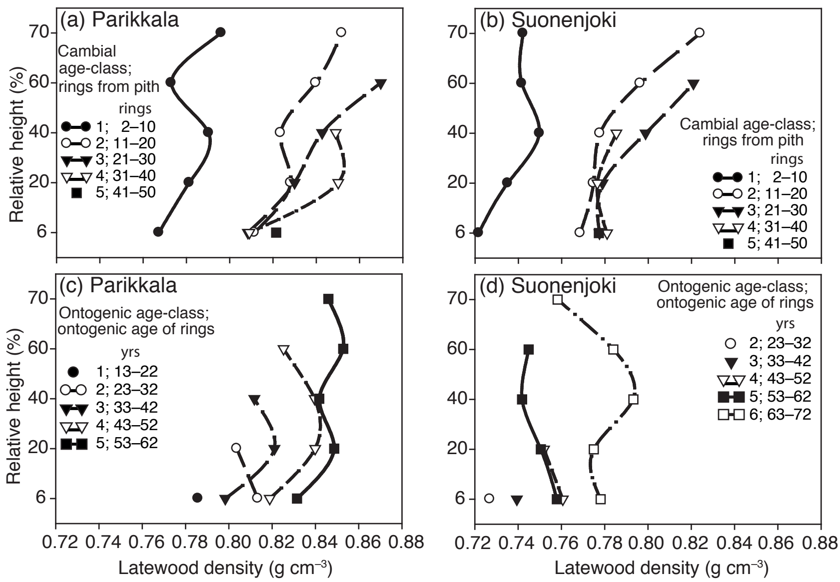

Fig. 6. Latewood density along the stem in different cambial (a, b) and ontogenic age-classes (c, d) in Parikkala (a, c) and Suonenjoki (b, d) (for an explanation of cambial and ontogenic age-classes, see Fig. 1 and Table 2).

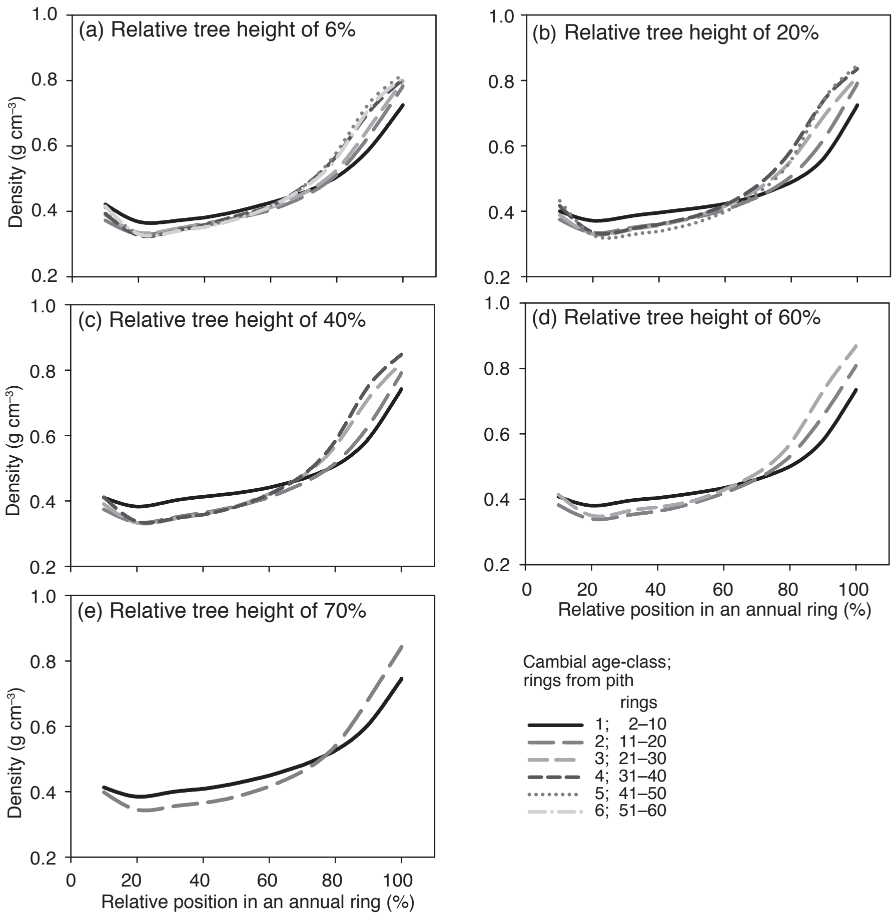

Fig. 7. The intra-ring variation of wood density in different cambial age-classes along the stem plotted against the relative position in an annual ring (for an explanation of cambial age-classes, see Fig. 1 and Table 2). The data from Parikkala and Suonenjoki are combined.

RD decreased with increasing TH (Fig. 4), ED varied only slightly (Fig. 5) and LD was highly variable between various TH (Fig. 6).

3.3 Intra-Ring Variation of Wood Density

As averaged over the whole data set, WD in the first formed earlywood within an annual ring was 0.396 ± 0.096 g cm^{-3} (mean ± SD). Thereafter, WD slightly decreased with the increasing distance from the ring boundary, reaching the minimum value (0.350 ± 0.056 g cm^{-3}) at the relative distance of 20% from the ring boundary (Fig. 7). After that, WD continuously increased towards latewood. At the relative distance of about 70%, the rate of increase speeded up and the faster increase rate continued towards the end of the ring.

In the first formed earlywood, WD was higher in the rings near the pith than in the outer rings. In the outer rings, however, WD increased faster towards latewood. Thus, the largest intra-ring variation of WD was in the outermost rings. In addition, the LW% was higher in the outer rings than in the rings near the pith.

Table 4. Correlation coefficients between ring width and wood density components at different relative heights (TH; %) in the tree. Data from Parikkala and Suonenjoki are combined.

TH	RW vs. LW%	RW vs. RD	RW vs. RD[p]	RW vs. ED	RW vs. LD	LW% vs. RD	LW% vs. ED	LW% vs. LD	RD vs. ED	RD vs. LD	ED vs. LD
70%	–0.38*	–0.35*	–0.17*	–0.11*	–0.45*	0.59*	0.34*	0.33*	0.91*	0.61*	0.38*
60%	–0.53*	–0.49*	–0.23*	–0.23*	–0.45*	0.62*	0.31*	0.29*	0.89*	0.60*	0.32*
40%	–0.57*	–0.50*	–0.20*	–0.21*	–0.38*	0.66*	0.32*	0.28*	0.86*	0.59*	0.36*
20%	–0.61*	–0.50*	–0.15*	–0.21*	–0.32*	0.68*	0.35*	0.22*	0.86*	0.57*	0.37*
6%	–0.48*	–0.52*	–0.32*	–0.34*	–0.26*	0.63*	0.35*	0.16*	0.89*	0.60*	0.46*

RW, ring width; LW%, latewood percentage; RD, average wood density of individual annual rings; ED, earlywood density; LD, latewood density; *, $P \leq 0.01$; [p] Partial correlation between RW and RD, controlling for LW%.

Table 5. Correlation coefficients between ring width and wood density components in different cambial age-classes. Data from Parikkala and Suonenjoki are combined.

Cambial age-class	RW vs. LW%	RW vs. RD	RW vs. RD[p]	RW vs. ED	RW vs. LD	LW% vs. RD	LW% vs. ED	LW% vs. LD	RD vs. ED	RD vs. LD	ED vs. LD
1	–0.46*	–0.47*	–0.32*	–0.34*	–0.21*	0.49*	0.31*	0.07*	0.95*	0.49*	0.37*
2	–0.46*	–0.53*	–0.33*	–0.41*	–0.37*	0.70*	0.48*	0.28*	0.92*	0.68*	0.58*
3	–0.40*	–0.51*	–0.35*	–0.42*	–0.22*	0.69*	0.46*	0.17*	0.91*	0.61*	0.49*
4	–0.30*	–0.45*	–0.36*	–0.39*	–0.14*	0.64*	0.39*	0.06°	0.89*	0.58*	0.45*
5	–0.30*	–0.44*	–0.35*	–0.45*	–0.07	0.64*	0.39*	0.08°	0.90*	0.60*	0.45*

RW, ring width; LW%, latewood percentage; RD, average wood density of individual annual rings; ED, earlywood density; LD, latewood density; *, $P \leq 0.01$; °, $P \leq 0.05$; [p] Partial correlation between RW and RD, controlling for LW%.

Table 6. Correlation coefficients between ring width and wood density components in different ontogenic age-classes. Data from Parikkala and Suonenjoki are combined.

Ontogenic age class	RW vs. LW%	RW vs. RD	RW vs. RD[p]	RW vs. ED	RW vs. LD	LW% vs. RD	LW% vs. ED	LW% vs. LD	RD vs. ED	RD vs. LD	ED vs. LD
1	–0.50*	–0.60*	–0.46*	–0.47*	–0.19*	0.52*	0.33*	–0.03	0.93*	0.46*	0.34*
2	–0.39*	–0.33*	–0.17*	–0.19*	–0.14*	0.49*	0.28*	0.10*	0.93*	0.51*	0.38*
3	–0.50*	–0.51*	–0.28*	–0.33*	–0.33*	0.64*	0.39*	0.26*	0.91*	0.63*	0.45*
4	–0.58*	–0.53*	–0.24*	–0.26*	–0.42*	0.68*	0.35*	0.30*	0.87*	0.63*	0.43*
5	–0.55*	–0.51*	–0.25*	–0.26*	–0.39*	0.64*	0.31*	0.22*	0.87*	0.61*	0.41*
6	–0.52*	–0.46*	–0.17*	–0.23*	–0.20*	0.69*	0.38*	0.11*	0.88*	0.55*	0.42*

RW, ring width; LW%, latewood percentage; RD, average wood density of individual annual rings; ED, earlywood density; LD, latewood density; *, $P \leq 0.01$; [p] Partial correlation between RW and RD, controlling for LW%.

3.4 Relationship Between Wood Density Components

The correlation coefficients between WD components at different TH are presented in Table 4. The negative correlation between RD and RW decreased with increasing TH. Accordingly, the positive correlation between RD and LW% slightly decreased with increasing TH. In contrast, the positive correlations of RD with ED and LD tended to slightly increase with TH.

The correlations between WD components in different cambial and ontogenic age-classes are listed in Tables 5 and 6, respectively. The negative correlation between RD and RW decreased with the increasing cambial age-class, but varied among ontogenic age-classes. Accordingly, the positive correlation between RD and LW% decreased with the increasing cambial age, but increased with the increasing ontogenic age-class. Furthermore, the positive correlations of RD with ED and LD tended to be lower with the increasing cambial age-class, but higher with the increasing ontogenic age-class. The partial correlations between WD and RW, controlling the effect of LW%, were negative and statistically significant, but lower than the simple correlations between WD and RW.

4 Discussion

4.1 Within-Stem Variation in Wood Density

The results showed that the random variation between trees accounted for 5–21% of the total variation in WD (while analysed independent of the effect of radial growth rate, i.e., ring width). The between-tree variation was at least partly due to genetic variation among individual trees (cf. Bergstedt and Olesen 2000). RD and its components – ED and LD, as well as LW% – are under moderate to high genetic control (Hannrup et al. 2001, Raiskila et al. 2006). In 19-year-old clonal trials of Norway spruce in southern Sweden, Hannrup et al. (2004) found high broad-sense heritability values for RD (0.36–0.55), ED (0.33–0.51) and LD (0.30–0.56).

In our study, the variation between annual rings accounted also for a large part (11–27%) of the variation, while TH accounted only for 3–6% of the total variation in WD. In Saranpää (2003), the average WD of 240 Norway spruce trees was studied at different heights in the stem. The distance from the pith and height in the tree accounted for only a minor part of the total variation in WD (ca.1%), while the random between-stem and within-stem variation accounted for the largest part of the variation (ca. 34% and 30%, respectively). Similarly, Wilhelmsson et al. (2002) reported that stem diameter, number of annual rings and climatic indices as fixed factors accounted for about 50% of the variation in WD of Norway spruce, while random within-tree variation accounted for the remaining variation for WD. For 31- and 47-year-old Norway spruce trees in Denmark, Danborg (1994) found two major sources of variation in RD: RD decreasing with increasing RW, and RD decreasing from the pith outwards to ring number 10 after which RD fluctuated due to weather variations. Moreover, Danborg (1994) found a large annual variation both in ED and LD due to weather variations.

In our study, RD from the pith outwards followed the well-documented development for Norway spruce: decreasing from near the pith to the lowest value in the rings 10–20 and then increasing towards the outer sapwood (e.g., Hakkila 1966, Olesen 1977, Danborg 1994, Saranpää 1994, Lindström 1996). Moreover, the variation in RD from the pith outwards was similar at different TH. The decrease in RD from the pith outwards was mainly due to a decrease in earlywood density (ED). This is in accordance with the result of Danborg (1994), who reported that the decrease in RD from the pith towards ring number 10 was due to decreasing ED.

The demarcation of juvenile and mature wood of Norway spruce has been defined to occur around ring number 10 from the pith (Danborg 1994, Saranpää 1994). Juvenile wood is produced near the pith by a young cambium, whereas mature wood is produced by more mature cambium farther from the pith (Kucera 1994, Larson 1994). The within-stem changes in WD found in this study were relatively smaller than the within-stem changes in RW and LW%. Also for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and balsam fir (*Abies balsamea* (L.) Mill.), the within-stem changes in WD were reported to be smaller than the within-stem changes in RW and LW% (Abdel-Gadir et al. 1993, Koga and Zhang 2004).

In the present study in a given cambial age, WD increased with increasing TH. This increase in WD was related to concurrent decrease in RW and increase in LW% with the increasing TH. Petty et al. (1990) studied WD of 48-year-old Norway spruce trees from the pith outwards at different TH. They found that in the given radial position from the pith, WD slightly increased from the stem base to the tree top. Also Saranpää (2003) reported an increase in WD from the breast height to the height of 15 m in given radial positions. Moreover, in given cambial age, Molteberg and Høibø (2006) found increasing WD with increasing TH for 28-year-old Norway spruce trees.

The vascular cambium matures with tree age due to maturation processes in the apical meristem at the time of cambium formation (cyclophysis) and the processes taking place in the cambium after its formation (Olesen 1978, 1982). Cambial maturity is primarily determined by the number of cambial cell divisions (Philipson and Butterfield 1967, Sirviö and Kärenlampi 2001). Increasing WD along the stem at the same cambial age, found in this and other studies, is most likely caused by the maturation processes in the apical meristem. Thus, at the same cambial age, wood produced near the stem apex is ontogenetically older than that produced near the stem base (Schweingruber et al. 2006).

For a given ontogenic age, we found a decreasing WD with increasing TH, related to increasing RW and decreasing LW% along the stem. This development in WD along the stem is probably due to the higher amount of juvenile wood at the tree top compared to that at the lower parts of the stem.

In most of the studies on Norway spruce, the mean WD of cross-sectional discs was measured at various heights. However, the results from these studies differ. Some authors reported a slight increase in WD from the stump to about 50% of tree height, above which WD decreases towards the top (Hakkila and Uusvaara 1968, Olesen 1982, Johansson 1993). The opposite has also been reported: a slight decrease in WD from the stem base to 30–50% of tree height, and then a steady increase upwards (Hakkila 1966, Atmer and Thörnqvist 1982 (only one stem analysed), Frimbong-Mensah 1987, Repola 2006). The disparity of the results may partly be due to different sampling practices and sample sizes (Heger 1974, Molteberg and Høibø 2006). Different silvicultural operations may also affect the axial variation in WD.

4.2 Intra-Annual Variation in Wood Density Along the Stem

In this study, the intra-ring variation was the major (up to 80%) source of the variation in WD. Decoux et al. (2004) have reported that WD exhibits maximum variance within individual annual rings, ranging from ca. 300 to 1000 kg m^{-3}. We found that within individual annual rings, WD decreased from near the ring boundary outwards to about 20% relative distance from the boundary. After that, WD increased towards latewood, and the rate of increase speeded up at 70% relative distance from the boundary. Our finding is in accordance with earlier results. A small decrease in WD at the beginning of annual ring, prior to the phase of low WD, followed by a quick increase was reported for Norway spruce and Scots pine (*Pinus sylvestris* L.) by Deleuze and Houllier (1998). Similarly, for Douglas fir, Rathgeber et al. (2006) found a slight decrease of 10% at the beginning of ring and an increase of 212% thereafter.

We found that within annual rings, the difference between ED and LD was larger in the outer rings than in the rings near the pith. The increase in WD from the pith outwards was related to the increasing LD and LW%. Similar findings were also reported for radiata pine (*Pinus radiata* D. Don; Walker and Dodd 1988) and balsam fir (Koga and Zhang 2004). The variation in WD between early- and latewood may be heritable (Kennedy 1966, Abdel-Gadir et al. 1993). WD is also reported to be rather constant in earlywood, but fluctuate more in latewood due to, e.g., climatic characteristics (e.g., Heger et al. 1974, Olesen 1982, Bouriaud et al. 2005).

The changes in intra-ring WD from earlywood towards latewood are mainly due to the changes in tracheid dimensions (Kellogg and Wangaard 1969, Skaar 1988). The Norway spruce wood consists mostly (94%) of longitudinal tracheids that are derived from cambial fusiform initials (Petric and Scukanec 1973, Siau 1984). In the present study, the resolution of the WD measurements, i.e., the size of the measured pixels was 25.4 μm. Thus, the resolution was in a near proximity of the average sizes of Norway spruce tracheids: the radial tracheid diameter decreases from about 40 μm in earlywood to about 10 μm in latewood (Fengel 1969, Jaakkola et al. 2005b, 2007).

The cambial activity during the growing season is the key process in determining the tracheid anatomical characteristics, and further, the intra-ring variation in WD (Mitchell and Denne 1997). The intra-ring variation in tracheid dimensions is found to be larger in the outer rings than near the pith (Herman et al. 1998b, Mäkinen et al. 2002a). For Douglas fir, model simulations showed that the increase in WD from earlywood to latewood is mainly due to the thickening in tangential and radial cell walls and reduced tracheid diameter in the radial direction (Rathgeber et al. 2006). However, changes in tracheid characteristics did not account for all the changes in WD in Douglas fir (Rathgeber et al. 2006) and Sitka spruce (*Picea sithensis* (Bong.); Mitchell and Denne 1997).

4.3 Relationship Between Wood Density Components

Correlation coefficients between RD, ED, LD, RW and LW% had no large differences between TH and radial positions in the stem. However, we found decreasing negative correlations between RD and RW with cambial age, as well as with increasing TH. Zhang (1998) reported a similar decreasing negative correlation between RD and RW with increasing cambial age for black spruce (*Picea mariana* (Mill.) B.S.P.). In addition, Koga and Zhang (2004) found a slight tendency for lower correlation between RD and RW with increasing stem height in balsam fir.

In this study, the partial correlation between RD and RW, controlling for LW%, was lower (r_p = –0.17 – –0.46, $P \leq 0.01$) than the simple correlation (r = –0.33 – –0.6, $P \leq 0.01$). Similarly, Wimmer and Downes (2003) reported that the partial correlation between RD and RW of 70-year-old Norway spruce trees was lower as compared to simple correlation. The negative relation between RW and WD is thus indirect and diminishes with constant LW%. Wimmer and Downes (2003) also found that the correlation between RD and RW fluctuates between calendar years according to weather variation (e.g., precipitation and temperature) and silvicultural operations (e.g., thinning and fertilisation).

Conclusions

The detailed analyses of this study verified our knowledge of the variation in WD and enable us to make more reliable models to predict WD in Norway spruce. The between-tree variation in WD of Norway spruce was lower than the within-tree variation. The inter-ring variation accounted for a larger part of the variation in WD than the variation between TH. Variation within annual rings was the major source of variation in WD. The difference in WD between earlywood and latewood was smaller in the rings near the pith than in the outer rings. The increasing WD from the pith outwards was related to the increasing LD and LW%, whereas ED remained almost constant from the pith to the bark. Understanding the variation in WD can lead to practical benefits while sorting wood raw material for different end-uses in forest industry.

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References

Abdel-Gadir, A.Y., Krahmer, R.L. & McKimmy, M.D. 1993. Relationships between intra-ring variables in mature Douglas-fir trees from provenance plantations. Wood and Fiber Science 25(2): 182–191.

Atmer, B. & Thörnqvist, T. 1982. Fiberegenskaper i gran (Picea abies Karst.) och tall (Pinus sylvestris L.). The properties of tracheids in spruce (Picea abies Karst.) and pine (Pinus sylvestris L.). The Swedish University of Agricultural Sciences, Department of Forest Products, Report 134. 59 p.

(In Swedish with English summary).
Bergstedt, A. & Olesen, P.O. 2000. Models for predicting dry matter content of Norway spruce. Scandinavian Journal of Forest Research 15(6): 633–644.
Bouriaud, O., Leban, J.-M., Bert, D. & Deleuze, C. 2005. Intra-annual variations in climate influence growth and wood density of Norway spruce. Tree Physiology 25(6): 651–660.
Cajander, A.K. 1949. Forest types and their significance. Acta Forestalia Fennica 56. 71 p.
Danborg, F. 1994. Density variation and demarcation of the juvenile wood in Norway spruce. Danish Forest and Landscape Research Institute, Forskningserien 10: 1–78.
Decoux, V., Varcin, É. & Leban, J.-M. 2004. Relationships between the intra-ring wood density assessed by X-ray densitometry and optical anatomical measurements in conifers. Consequences for the cell wall apparent density determination. Annals of Forest Science 61: 251–262.
Deleuze, C. & Houllier, F. 1998. A simple process-based xylem growth model for describing wood microdensitometric profiles. Journal of Theoretical Biology 193: 99–113.
Duff, G.H. & Nolan, N.J. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in Pinus resinosa Ait. Canadian Journal of Botany 13: 471–513.
Dutilleul, P., Herman, M. & Avella-Shaw, T. 1998. Growth rate effects on correlations among ring width, wood density, and mean tracheid length in Norway spruce (Picea abies). Canadian Journal of Forest Research 28(1): 56–68.
Ekman, R. 1980. Wood extractives in Norway spruce: a study of nonvolatile constituents and their effects on Fomes annosus. Publications of the Institute of Wood Chemistry and Pulp and Paper Technology A 330: 1–186.
Fengel, D. 1969. The ultrastructure of cellulose from wood. Part I: Wood as the basic material for the isolation of cellulose. Wood Science and Technology 3: 203–217.
Frimbong-Mensah, K. 1987. Fibre length and basic density variation in the wood of Norway spruce (Picea abies L. Karst.) from northern Norway. Communications of the Norwegian Forest Research Institute 40: 1–25.
Gustavsen, H. 1980. Site index curves for conifer stands in Finland. Folia Forestalia 454: 1–31. (In Finnish with English summary).
Hakkila, P. 1966. Investigations on the basic density of Finnish pine, spruce and birch wood. Communicationes Instituti Forestalis Fenniae 61: 1–98.
— & Uusvaara, O. 1968. On the basic density of plantation-grown Norway spruce. Communicationes Instituti Forestalis Fenniae 66: 1–23.
Hannrup, B., Danell, Ö., Ekberg, I. & Moëll, M. 2001. Relationships between wood density and tracheid dimensions in Pinus sylvestris L. Wood and Fiber Science 33(2): 173–181.
— , Cahalan, C., Chantre, G., Grabner, M., Karlsson, B., Le Bayon, I., Jones, G.L., Müller, U., Pereira, H., Rodrigues, J.C., Rosner, S., Rozenberg, P., Wilhelmsson, L. & Wimmer, R. 2004. Genetic parameters of growth and wood quality traits in Picea abies. Scandinavian Journal of Forest Research 19: 14–29.
Heger, L. 1974. Longitudinal variation of specific gravity in stems of black spruce, balsam fir, and lodgepole pine. Canadian Journal of Forest Research 4(3): 321–326.
— , Parker, M.L. & Kennedy, R.W. 1974. X-ray densitometry: A technique and an example of application. Wood Science 7(2): 140–148.
Herman, M., Dutilleul, P. & Avella-Shaw, T. 1998a. Growth rate effects on temporal trajectories of ring width, wood density, and mean tracheid length in Norway spruce (Picea abies (L.) Karst.). Wood and Fiber Science 30(1): 6–17.
— , Dutilleul, P. & Avella-Shaw, T. 1998b. Intra-ring and inter-ring variations of the tracheid length in fast-grown versus slow-grown Norway spruce (Picea abies). IAWA Journal 19(1): 3–23.
Hochberg, Y. 1988. A sharper Bonferroni procedure for multiple tests of significance. Biometrika 75: 800–802.
Holmbom, B., Ekman, R., Sjöholm, R., Eckerman, C. & Thornton, J. 1991. Chemical changes in peroxide bleaching of mechanical pulps. Papier 45: V16.
Jaakkola [Jyske], T., Mäkinen, H. & Saranpää, P. 2005a. Wood density in Norway spruce: changes with thinning intensity and tree age. Canadian Journal of Forest Research 35(7): 1767–1778.
— , Mäkinen, H., Sarén, M.-P. & Saranpää, P. 2005b. Does thinning intensity affect the tracheid dimensions of Norway spruce? Canadian Journal of Forest Research 35(11): 2685–2697.
— , Mäkinen, H. & Saranpää, P. 2006. Wood density of Norway spruce: Responses to timing and intensity of first commercial thinning and fertilisa-

tion. Forest Ecology and Management 237(1–3): 513–521.
— , Mäkinen, H. & Saranpää, P. 2007. Effects of thinning and fertilisation on tracheid dimensions and lignin content of Norway spruce. Holzforschung 61: 301–310.
Johansson, K. 1993. Influence of initial spacing and tree class on the basic density of Picea abies. Scandinavian Journal of Forest Research 8(1): 18–27.
Kellogg, R.M., & Wangaard, F.F. 1969. Variation in the cell-wall density of wood. Wood and Fiber Science 1: 180–204.
Kennedy, R.W. 1966. Intra-increment variation and heritability of specific gravity, parallel-to-grain tensile strength, stiffness, and tracheid length, in clonal Norway spruce. Tappi Journal 49(7): 292–296.
Koga, S. & Zhang, S.Y. 2004. Inter-tree and intra-tree variations in ring width and wood density components in balsam fir (Abies balsamea). Wood Science and Technology 38(2): 149–162.
Kucera, B. 1994. A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. Wood and Fiber Science 26(1): 152–167.
Larson, P.R. 1994. The vascular cambium. Development and structure. Springer series in wood science. Springer-Verlag, Berlin-Heidelberg-New York. 725 p.
Lindström, H. 1996. Basic density in Norway spruce. Part I. A literature review. Wood and Fiber Science 28(1): 15–27.
Mäkinen, H., Saranpää, P. & Linder, S. 2002a. Effect of growth rate on fibre characteristics in Norway spruce (Picea abies (L.) Karst.). Holzforschung 56(5): 449–460.
— , Saranpää, P. & Linder, S. 2002b. Wood-density variation of Norway spruce in relation to nutrient optimization and fibre dimensions. Canadian Journal of Forest Research 32(2): 185–194.
— , Jaakkola, T., Saranpää, P. & Piispanen, R. 2007. Predicting wood and tracheid properties of Norway spruce. Forest Ecology and Management 241(1–3): 175–188.
Mitchell, M.D. & Denne, M.P. 1997. Variation in density of Picea sitchensis in relation to within-tree trends in tracheid diameter and wall thickness. Forestry 70(1): 47–60.
Molteberg, D. & Høibø, O. 2006. Development and variation of wood density, kraft pulp yield and fibre dimensions in young Norway spruce (Picea abies). Wood Science and Technology 40(3): 173–189.
Ojansuu, R. & Henttonen, H. 1983. Estimation of local values of monthly mean temperature, effective temperature sum and precipitation sum from measurements made by the Finnish Meteorological Office. Silva Fennica 17(2): 143–160.
Olesen, P.O. 1976. The interrelation between basic density and ring width of Norway spruce. Det Forstlige Forsøksvaesen i Danmark 34(4): 339–359.
— 1977. The variation of the basic density level and tracheid width within the juvenile and mature wood of Norway spruce. Forest Tree Improvement 12: 1–21.
— 1978. On cyclophysis and topophysis. Silvae Genetica 27(5): 173–178.
— 1982. The effect of cyclophysis on tracheid width and basic density in Norway spruce. Forest Tree Improvement 15: 1–80.
Panshin, A.J. & de Zeeuw, C. 1980. Textbook of wood technology. 4th ed. McGraw-Hill, New York. 722 p.
Pape, R. 1999. Influence of thinning and tree diameter class on the development of basic density and annual ring width in Picea abies. Scandinavian Journal of Forest Research 14: 27–37.
Petric, B. & Scukanec, V. 1973. Volume percentage of the tissues in wood of conifers grown in Yugoslavia. IAWA Bulletin 2: 3–7.
Petty, J.A., Macmillan, D.C. & Steward, C.M. 1990. Variation of density and growth ring width in stems of Sitka and Norway spruce. Forestry 63(1): 39–49.
Philipson, W.R. & Butterfield, B.G. 1967. A theory on the causes of size variation in wood elements. Phytomorphology 17: 155–159.
Raiskila, S., Saranpää, P., Fagerstedt, K., Laakso, T., Löija, M., Mahlberg, R., Paajanen, L. & Ritschkoff, A.-C. 2006. Growth rate and wood properties of Norway spruce cutting clones on different sites. Silva Fennica 40(2): 247–256.
Rathgeber, C.B.K., Decoux, V. & Leban, J.-M. 2006. Linking intra-tree-ring wood density variations and tracheid anatomical characteristics in Douglas fir (Pseudotsuga menziesii (Mirb.) Franco). Annals of Forest Science 63: 699–706.
Repola, J. 2006. Models for vertical wood density of Scots pine, Norway spruce and birch stems, and their application to determine average wood density. Silva Fennica 40(4): 673–685.
Saikku, O. 1975. The effect of fertilization on the

basic density of Scots pine (Pinus sylvestris L.). A densitometric study on the X-ray chart curves of the wood. Communicationes Instituti Forestalis Fenniae 85. 49 p.

Saranpää, P. 1994. Basic density, longitudinal shrinkage and tracheid length of juvenile wood of Picea abies. Scandinavian Journal of Forest Research 9(1): 68–74.

— 2003. Wood density and growth. In: Barnett, J.R. & Jeronimidis, G. (eds.). Wood quality and its biological basis. Blackwell Publishing & CRC Press, Biological Sciences Series, Bodmin, Great Britain. p. 87–117.

SAS Institute Inc. 2004. SAS/STAT® 9.1 User's Guide. Cary, NC: SAS Institute Inc. 5121 p.

Schweingruber, F.H., Börner, A. & Schulze, E.-D. 2006. Atlas of woody plants stems: evolution, structure, and environmental modifications. Springer, Berlin-Heidelberg. 229 p.

Siau, J.F. 1984. Transport processes in wood. Springer-Verlag, Berlin-Heidelberg-New York. 245 p.

Sirviö, J. & Kärenlampi, P. 2001. The effects of maturity and growth rate on the properties of spruce wood tracheids. Wood Science and Technology 35(6): 541–554.

Skaar, C. 1988. Wood-water relations. Springer-Verlag. Berlin-Heidelberg-New York. 283 p.

Vuokila, Y. & Väliaho, H. 1980. Growth and yield models for conifer cultures in Finland. Communicationes Instituti Forestalis Fenniae 99(2). 271 p. (In Finnish with English summary).

Walker, N.K. & Dodd, R.S. 1988. Calculation of wood density variation from X-ray densitometer data. Wood and Fiber Science 20: 35–43.

Wilhelmsson, L., Arlinger, J., Spångberg, K., Lundqvist, S.-O., Grahn, T., Hedenberg, Ö. & Olsson, L. 2002. Models for predicting wood properties in stems of Picea abies and Pinus sylvestris in Sweden. Scandinavian Journal of Forest Research 17: 330–350.

Wimmer, R. & Downes, G.M. 2003. Temporal variation of the ring width–wood density relationship in Norway spruce grown under two levels of anthropogenic disturbance. IAWA Journal 24(1): 53–61.

Zhang, S.Y. 1998. Effect of age on the variation, correlations and inheritance of selected wood characteristics in black spruce (Picea mariana). Wood Science and Technology 32(3): 197–204.

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