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Tracheid Wall Thickness and Lumen Diameter in Different Axial and Radial Locations in Cultivated *Larix sibirica* Trunks

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In *Larix* trunks the properties of wood differ clearly radially, but the axial differences are smaller as well as being less studied. Wood anatomy is in particular poorly studied, even though all other wood properties derive from cell and tissue structure. The aim of this study was to chart variation in tracheid size (double wall thickness (2CWT), diameter of lumen (RD)) within fast grown cultivated Siberian larch (*Larix sibirica* Ledeb.) trunks. The differences in 2CWT and RD were clear between earlywood (EW) and latewood (LW), 2CWT increasing clearly less in EW than in LW towards the bark, while RD stayed quite stable in LW but in EW increased markedly towards the bark. The difference in 2CWT between EW and LW increased towards the upper trunk. In conclusion, the radial variation in RD and 2CWT was different between the butt and other studied heights. As the difference in 2CWT between EW and LW was smaller at the butt than the upper portion of the trunk, the wood was the most homogenous at the butt.

Keywords earlywood, fibre, latewood, Siberian larch, wood, xylem
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1 Introduction

Radial variation of many wood properties due to the maturing of cambium is exceptionally large in trunks of *Larix* species (Hakkila and Winter 1973, Koizumi et al. 2003, 2005). Measured properties include wood density and annual ring width (Kärkkäinen 1978, Karlman et al. 2005), mechanical features (Juvonen et al. 1986, Grabner et al. 2005), extractives (Uprichard 1963, Côté et al. 1966, Gugnin et al. 1971, Hakkila and Winter 1973, Gierlinger and Wimmer 2004, Willför and Holmbom 2004) and anatomical characteristics (Neckhaichuk and Bryantseva 1984, Chui and MacKinnon-Peters 1995, Koizumi et al. 2003). Axial differences, including cell characteristics, are however smaller and poorly known (Chui and MacKinnon-Peters 1995, Luostarinen 2011a,b, Luostarinen and Heräjärvi 2011).

Cell characteristics affect processing and usage of wood through their influence on other wood properties. Even quite a small variation in cell properties may have practical effects. For example, the cell walls found in the upper portion of the trunk are thinner than those at the butt, which have been observed to cause an increased compaction ratio of the cells originating from the upper parts of trunks. Upper portions of trunks therefore give better medium density fibreboard (MDF), such as that manufactured from the wood of *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (Shi et al. 2007). The variation of anatomical characteristics within the trunks may therefore have unexpected impacts on products, and the axial knowledge, in addition to radial knowledge, of cell structure of wood is important. In particular, as the wood properties of the cultivated fast grown Siberian larch (*Larix sibirica* Ledeb.) are poorly studied, and as a major proportion of the larch plantations in Finland, totalling more than 30 000 ha (Lepistö and Napola 2005) are now at the age when the first thinning should be performed, information is needed about the wood properties of this species.

The aim of this study was to determine the radial and axial trends of tracheid size (wall thickness, diameter of lumen) changes in cultivated fast grown Siberian larch trees. The characteristics are discussed in comparison with other wood properties.

2 Materials and Methods

For this study, a total of 16 85-year-old *Larix sibirica* trees were used. The trees were felled from plantations owned by the Finnish Forest Research Institute, Punkaharju, Eastern Finland (61°81´N, 29°32´E), where the mean winter temperature is –5…–10 °C, mean summer temperature 15–20 °C and annual rainfall over 600 mm (World climate 2008). The stand was located on fertile mineral soil. The trees belonged to the Heikinheimo stand of Raivola provenience. The Raivola provenience has been one of the best cultivated in Finland according to growth, durability against many kind of damages, and the shape of trunk (Vuokila 1960, Mikola 1992, Silander et al. 2000, Lepistö and Napola 2005). The forest was planted in 1924 with four-year-old seedlings, and the stand was managed to produce logs of good quality. Mean height of the trees was 36.3 m at 71 years of age (Silander et al. 2000). The average trunk diameter at the butt was 47.9 cm ± 12.8 cm (standard error of the mean), at breast height 41.8 cm ± 1.1 cm, at 4.5 m 37.1 cm ± 11.8 cm, and at 9 m 36.0 cm ± 5.8 cm. Mean annual growth, wood density and proportion of latewood are presented in Table 1.

The trees were felled for studies of Mikkeli University of Applied Sciences concerning sawn Siberian larch timber (Heikkonen et al. 2007), and in the connection of felling, 5-cm-thick cross-cut discs were sawn from the butt, and at heights of 4.5 and 9 metres for this study. The chosen trees had at least 9 m long branchless butt suitable for sawing (no visible defects or deformations), which produced logs of Quality A, thus suitable for good quality carpenters' products.

The discs were left to dry at room temperature before strips were sawn in random directions from pith to bark to separate the specimens for anatomical measurements. Before anatomical examination, same strips were used for measuring Itrax-X-ray profiles, for which the wood had to be dried to get strips of appropriate dimensions, quality and moisture content. Radial locations based on cambial age were analysed. The studied radial locations were: 1–5 years (juvenile wood), 15–20 years (maturing wood), and two locations in mature wood (sampling in batches of 10 rings). The exact position of the two mature wood

Table 1. Averages ± standard errors of the mean of densities (at moisture content of 12%), ring widths and proportions of latewood by height and wood age class (years from the pith).

Height	Wood age, years	Density, kg/m^3	Ring width, mm	Proportion of latewood, %
Butt	1–5	386.4 ± 12.3	3.4 ± 0.3	38.5 ± 1.7
	15–20	418.1 ± 11.4	4.2 ± 0.3	39.5 ± 2.2
	21–40	454.0 ± 10.3	2.2 ± 0.2	48.5 ± 1.9
	41–60	476.7 ± 11.9	2.6 ± 0.3	54.5 ± 2.0
	61–73	454.1 ± 12.8	3.0 ± 0.3	54.1 ± 2.7
4.5 m	1–5	375.9 ± 13.7	6.6 ± 0.4	23.9 ± 2.3
	15–20	426.7 ± 8.8	2.7 ± 0.2	45.3 ± 2.1
	21–40	453.1 ± 8.7	1.8 ± 0.1	48.5 ± 1.6
	41–60	474.0 ± 8.0	1.6 ± 0.1	54.2 ± 1.4
9.0 m	1–5	360.5 ± 8.2	6.3 ± 0.4	20.2 ± 1.0
	15–20	417.3 ± 5.9	3.0 ± 0.2	37.4 ± 1.3
	21–40	440.5 ± 8.1	1.9 ± 0.1	42.6 ± 1.3
	41–60	435.4 ± 9.2	1.6 ± 0.1	49.7 ± 1.9

specimens depended on the size of the disc (which depended on height), and they were grouped by cambial age into three groups as follows: 21–40, 41–60 and 61–73 years. The number of samples therefore varied, from a minimum of eight to a maximum of 18 for the cambial age group of 21–40 years at the height of 9 m, because two of the trees had only ca. 40 rings at that height and thus both mature wood samples taken belonged to this cambial age group.

The wood samples were softened by boiling them in water for 45 min, but they remained hard to cut after boiling. They were therefore placed in a mixture of deionized water, 95% ethanol and glycerol (1:1:3) for further softening (Schmitz 2010). The samples were first retained in this mixture overnight at 60 °C, then at room temperature, until cross-cuts were taken as wet, directly after taking them from the solution. Microm rotary microtome with low profile metal blades (Leica 819) was used for cutting sections of thickness of 20 µm. The sections were dyed with safranin–alcian blue (Fagerstedt et al. 1996) and mounted with Depex.

From the sections, measurements were taken of tracheid double wall thickness from the radial walls (2CWT), both from earlywood (EW) and latewood (LW), as well as the radial diameter of lumen (RD) of tracheids from EW and LW, using Image Pro software, Leitz 12 Laborlux microscope and Sony DXC-905P 3CCD color video camera. Both parameters were measured from ten cells (twice from the same ring in juvenile and maturing wood, once per ring in mature wood) of each specimen and both wood types with accuracy of 0.001 µm. The measured cells were chosen from the same radial line so, that the measured EW cell located ca. 20 cells from the border of the annual ring, and the measured LW cell ca. 10 cells from the ring border. From juvenile and maturing wood, as two cells from both EW and LW were measured from each ring, they were measured radially from the same scene so that at least 5 cells were between the measured cells. This way the cells were always of wanted type, as border of EW and LW was determined earlier with the aid of Itrax x-ray densitometry (the mean of the maximum and minimum intraring densities were used as the threshold for EW and LW in each ring: the value above this threshold represented LW and the values below represented EW; see Luostarinen 2011a).The result for a sample is the mean of the ten measurements. The difference in 2CWT between EW and LW was calculated.

Differences in cell dimensions (dependent variables) between axial or radial locations (fixed factors), as well as any possible interaction between axial and radial locations in cell dimensions, were calculated using General Linear Model (GLM) Multivariate analysis in SPSS (version 19) using full factorial model. The pair-wise comparisons made between different axial or radial locations were performed using the Tukey HSD test. The pair-wise comparisons were undertaken only if no interaction between axial and radial locations was observed.

3 Results

Both radial and axial trend of 2CWT and RD were studied. 2CWT of EW ranged from 3.9–5.7 µm at the butt, 3.5–4.2 µm at 4.5 m and 2.7–3.7 µm at 9 m, and that of LW from 6.0–11.3 µm at the butt, 7.1–13.6 µm at 4.5 m, and 6.4–14.4 µm at 9 m (Fig. 1a, b). The RD of EW was 20.7–38.3 µm at the butt, 26.3–41.3 µm at 4.5 m, and 30.1–42.2 µm at 9 m, and of LW 9.0–9.7 µm at the butt, 9.1–10.7 µm at 4.5 m and 8.8–11.7 µm at 9 m, decreasing from juvenile wood towards the bark at 4.5 and 9 m (Fig. 2a, b). According to the GLM, interactions were observed between the effects of axial and radial location in 2CWT of LW, and in RD of EW (Table 2). 2CWT of LW increased radially at 4.5 and 9 m towards the outermost rings, but at the butt a decrease was observed after 40 years (Fig. 1b). Furthermore, RD of EW increased radially at all heights, remaining lowest at the butt (Fig. 2a). In contrast, no interaction between radial and axial locations was observed in 2CWT of EW, or in RD of LW. Some radial differences, however, were observed in 2CWT of EW: at the butt and at the height of 9 m 2CWT of juvenile wood was less than in any other cambial age group in EW. In addition, axial differences were observed in 2CWT of EW: in juvenile wood 2CWT of EW was less at 9 m than at the butt and 4.5 m, and in mature wood it was less at 4.5 m and 9 m than at the butt (Fig. 1a, Table 2). RD of LW differed radially in wood located at the heights of 4.5 and 9 m: in LW RD of juvenile wood was larger than that of cambially 21–40 years old wood. In addition, RD was axially larger at 9 m than at the butt in juvenile wood (Fig. 2b, Table 2).

The relationship between 2CWT and RD was different in EW than in LW, and at different cambial ages and heights (Figs. 3, 4). In LW, a very small increase in RD caused a large increase in 2CWT at most heights and cambial ages (Fig. 3a, b, c). However, at the butt the relationships were very different at each studied cambial age (Fig. 3a). At the butt height at the cambial ages 15–20 and 41–60 years the walls were the thinner the larger were the lumens, while at other cambial ages the relationship was opposite. At the heights of 4.5 and 9 m 2CWT increased when RD increased at all studied cambial ages (Fig. 3b, c); however, the increase in 2CWT was very small in juvenile wood at the height of 9 m. In EW, as well, 2CWT increased when RD increased

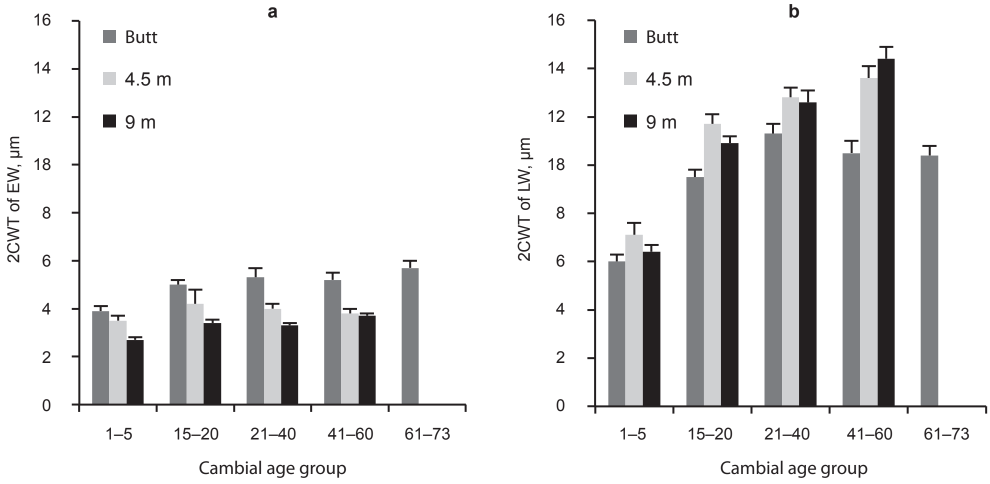

Fig. 1. Double cell wall thickness (2CWT) (µm) a) in earlywood (EW) and b) in latewood (LW) by cambial age groups and heights. Bars – standard error of the mean.

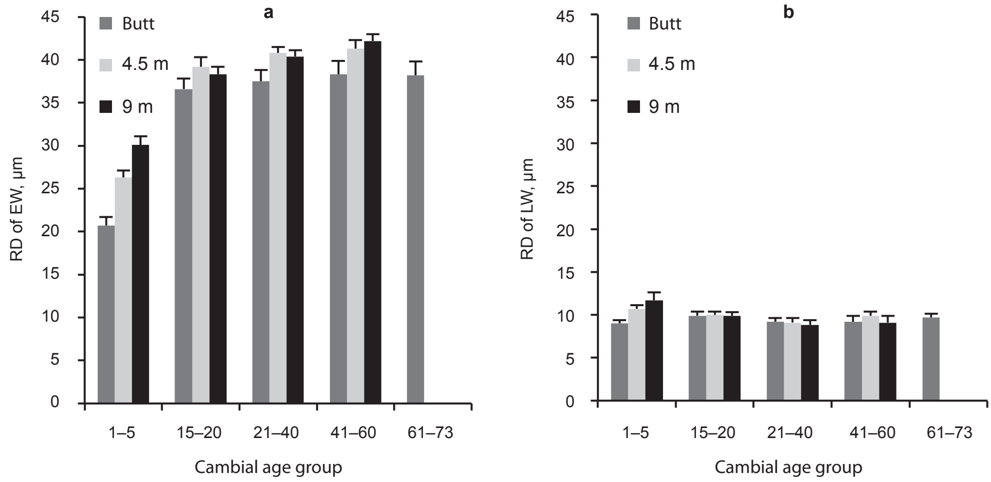

Fig. 2. Radial diameter of lumen (RD) (µm) a) in earlywood (EW) and b) in latewood (LW) by cambial age groups and heights. Bars – standard error of the mean.

Table 2. F-values calculated using GLM for the interaction of radial and axial effects and for radial and axial main effects. ** – significant at 0.01 level, * – significant at 0.05 level, ns – not significant. Statistically significant pair-wise comparisons are listed if radial or axial differences were observed without interaction. 2CWT – double cell wall thickness, RD – radial diameter of lumen, EW – earlywood, LW – latewood.

Parameter	Wood type	F(Radial*axial)	F(Radial)	F(Axial)
2CWT	EW	0.955ns	7.816**	34.652**
	EW		Butt: 1–5 vs 15–20*	1–5: Butt vs 9 m**
	EW		Butt: 1–5 vs 21–40**	1–5: 4.5 m vs 9 m*
	EW		Butt: 1–5 vs 41–60*	15–20: Butt vs 9 m*
	EW		Butt: 1–5 vs 61–73**	21–40: Butt vs 4.5 m**
	EW		9 m: 1–5 vs 15–20**	21–40: Butt vs 9 m**
	EW		9 m: 1–5 vs 21–40**	41–60: Butt vs 4.5 m**
	EW		9 m: 1–5 vs 41–60**	41–60: Butt vs 9 m**
	LW	2.620*	105.556**	23.763**
RD	EW	3.055**	112.833**	19.765**
	LW	1.850ns	2.879*	1.301ns
	LW		4.5 m: 1–5 vs 21–40*	
	LW		9 m: 1–5 vs 21–40*	1–5: Butt vs 9 m*
Difference in 2CWT (LW–EW)		2.875*	70.509**	62.323**

in most of the cases (Fig. 4a, b, c). However, the increase in 2CTW by increasing RD was clearly smaller in EW than in LW. At the butt the 2CWT even decreased when RD increased at the cambial ages of 21–40 and 41–60 years (Fig. 4a). At the heights of 4.5 and 9 m the relationships were positive at each cambial age, 2CWT always slightly increasing when RD increased (Figs. 4b, c).

The difference between 2CWT of EW and LW also revealed an interaction between axial and radial location (Fig. 5, Table 2). The difference increased with maturity, but at the butt it began again to decrease in mature wood. Conversely, at higher locations, the difference continued to increase, reaching ca. 10 µm at the cambial age of 41–60 years.

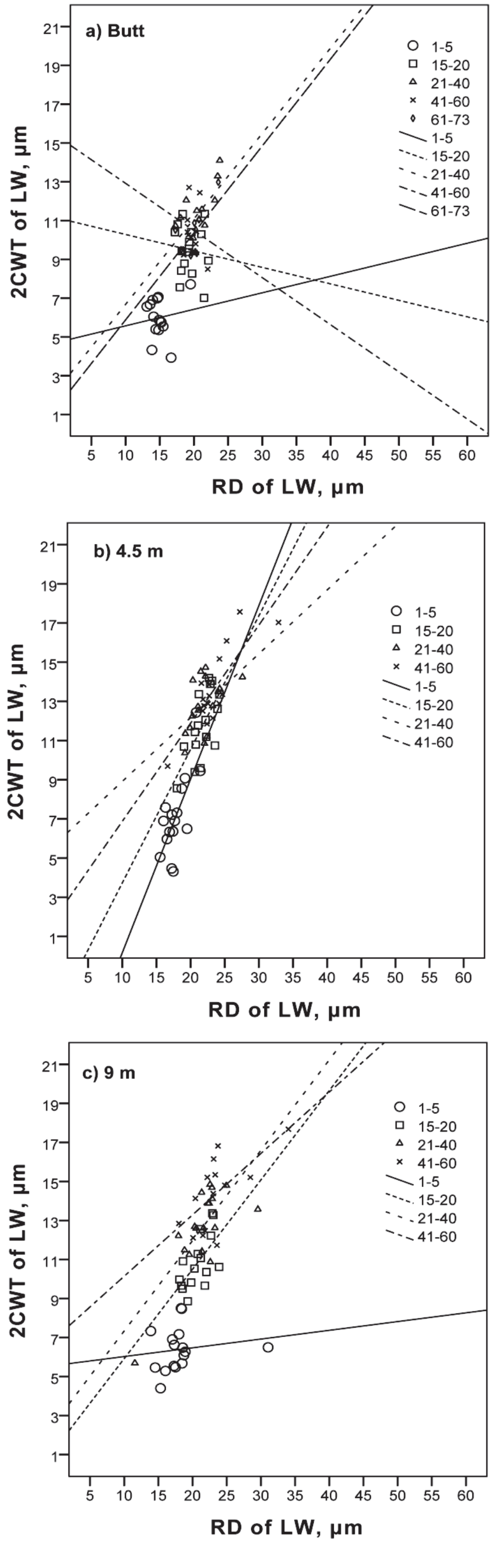

Fig. 3. Relationship of double cell wall thickness (2CWT) to radial lumen diameter in latewood (LW) a) at the butt height, b) at the height of 4.5 m, and c) at the height of 9 m by cambial age group.

4 Discussion and Conclusions

In this study, RD was very different in EW (20.7–42.2 µm) than in LW (8.8–11.7 µm) for cultivated fast grown *L. sibirica*. Tracheid diameter (incl. walls) of *L. sibirica* has earlier reported to be around 34–65 µm in EW and 15–25 µm in LW (Martinsson and Lesinski 2007), which values are near to those of this study, if the RD and 2CWT are combined. RD of *L. decidua* P. Mill., instead, has been reported to be slightly higher, around 35.5–55.0 µm in EW and 4.6–21.4 µm in LW (Wagenführ 1996), than observed in the studied Siberian larches. The CWT of *L. sibirica* varied from ca. 1.4 to 2.8 µm, and from 3.0 to 7.2 µm, in EW and LW, respectively, in this study: these values are slightly smaller than those reported by Terziev and Zamaratskaia (2007; EW 3.3 µm, LW 6.6 µm), Vaganov et al. (2006; from 1.5 to 5.5 µm) and Martinsson and Lesinski (2007; EW from 2.3 to 4.8 µm, LW from 5.5 to 10.5 µm). The presented ranges are, however, large. Fast growth rate has been observed to increase the tracheid lumen diameter of *L. sibirica* (Yazaki et al. 2001) and *L. leptolepis* [Sieb. and Zucc.] A. Murr. (Koga et al. 1997). Furthermore, in *L. leptolepis* the fast growth rate increases tracheid wall thickness of EW and decreases that of LW (Koga et al. 1997). Instead, a more uniform tracheid wall thickness between EW and LW has been found in narrow rather than in wide rings of *Pinus resinosa* Ait. (Zhu et al. 2007), but no effect of growth rate on tracheid wall thickness or cell diameter has been observed in *L. decidua* (Petrik 1968). The growth rate of the larch trees of this study (Table 1, Luostarinen 2011a) was high when compared with larches grown in their natural habitats (juvenile wood ca. 3 mm/a, mature wood ca. 1 mm/a) (Koizumi et al. 2003). Therefore, the high growth rate, observed particularly in juvenile wood of the studied trees at the uppermost heights, in addition to cambial age, may have affected the cell dimensions of cultivated *Larix sibirica* in this study.

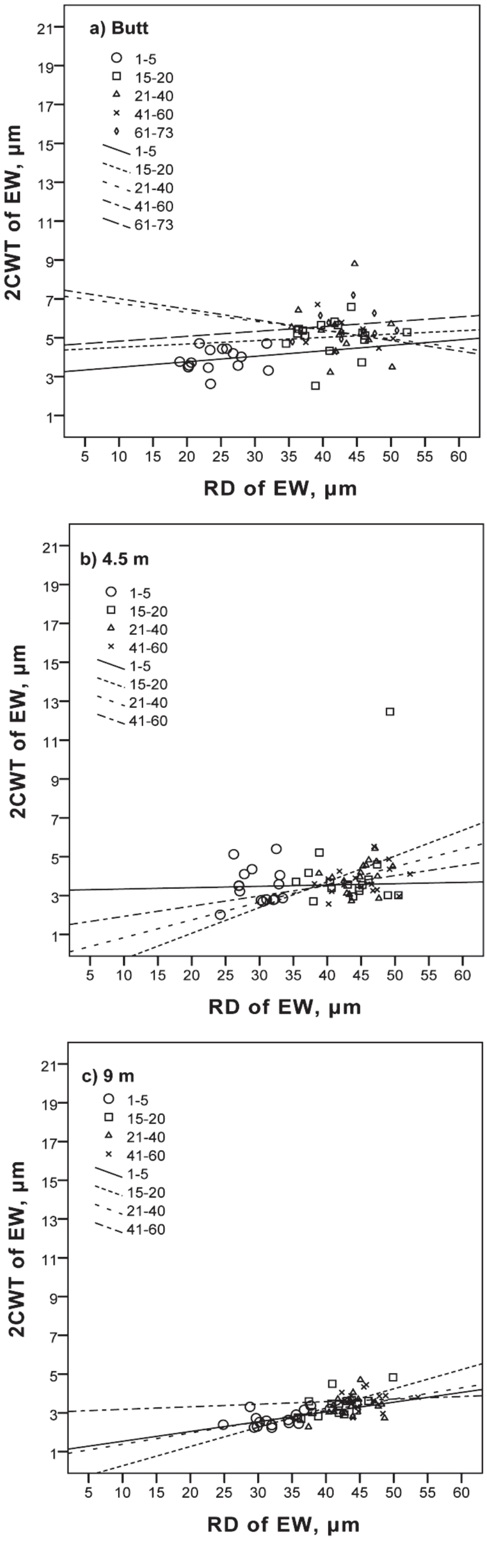

Fig. 4. Relationship of double cell wall thickness (2CWT) to radial lumen diameter in earlywood (EW) a) at the butt height, b) at the height of 4.5 m, and c) at the height of 9 m by cambial age group.

Radial trend in RD was observed in EW, but not in LW. The RD increased from pith to bark in EW. Combining RD and 2CWT would cause a radial trend, increasing from pith to bark, in whole cell diameter in both EW and LW, which is a common trend observed in softwoods (e.g. Lindström 1997, Mitchell and Denne 1997, Lenz et al. 2010, Franceschini et al. 2012). In *L. sibirica* the diameter of tracheids has been reported to increase from 30 µm of cambially 1–20 years old wood to 50 µm of cambially 100–120 years old wood (Khutorschikov and Zorina 1971). Instead, 2CWT increased from pith to bark in LW, but no trend was observed in EW. Similarly to the cultivated *L. sibirica* in this study, in Norway spruce (*Picea abies* (L.) H. Karst.) tracheid wall thickness of EW remained constant from juvenile to mature wood, while wall thickness of LW increased with maturation (Mitchell and Denne 1997). In addition, average tracheid wall thickness (EW and LW

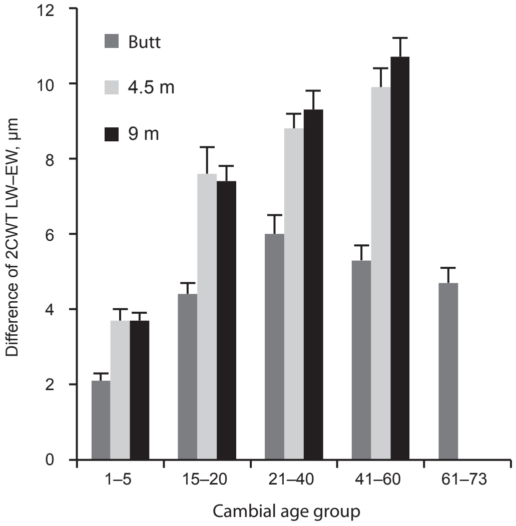

Fig. 5. Difference of double cell wall thickness (2CWT) between earlywood (EW) and latewood (LW) by cambial age group and height. Bars – standard error of the mean.

not separated) of *Pinus radiata* D. Don has been observed to increase from pith to bark (Lasserre et al. 2009). The 2CWT trends observed in this study follow the radial trends of both EW and LW density determined for the wood of *Larix sibirica* trees, while RD did not have comparable trend with density (Luostarinen 2011a). Even though density is the most important factor affecting mechanical properties of wood (Bodig and Jayne 1982), Müller et al. (2004) found only a minor effect of cell wall thickness and lumen diameter on shear strength in *Picea abies* wood: particularly in tangential-longitudinal stress, in which the fracture is parallel to rays, the thicker walls of LW than EW tracheids strengthen the wood, even though rays may affect in the opposite way. Additionally, the shear strength of larch wood increases from juvenile wood to mature heartwood, and decreases from the butt height to the height of 9 m in mature wood (Luostarinen and Heräjärvi 2011), which are in accordance with the thickening of, in particular, the LW cell walls. In addition, the slightly larger 2CWT of EW at the butt height than at the upper heights and negative ratios between RD and 2CWT from maturing to cambially 41–60 years old wood may be the reasons for the highest shear strength at the butt.

No statistically significant axial trend was observed in RD of LW. In EW, instead, RD increased towards the height of 9 m. In addition, axial trends were found for 2CWT: in EW the 2CWT was largest at the butt, but in LW it was smallest at the butt. Instead, Khutorschikov and Zorina (1971) measured cell diameters of 50 µm at the height of 1.3 m and 44 µm at the height of 16.5 m in Siberian larch, the trend thus being rather the opposite than in EW of this study. Furthermore, Mitchell and Denne (1997) found increase in cell diameter from the height of 1.3 m to the height of 60% for Sitka spruce (*Picea sitchensis* (Bong.) Carr). Thus, no results of same trees from both the heights of butt and 1.3 m concerning cell or lumen diameter were available, and it is not possible to assess whether the maximum of cell or lumen diameter is located upper than at the butt height. However, it is possible, as according to the information found by Kärkkäinen (2007), the maximum of fibre length can be found higher, moving upwards when the age of the tree increases. As the 2CWT of EW was largest and that of LW smallest at the butt, 2CWT was most uniform at this height, particularly in mature wood. In *L. sibirica* wood, the density variation between EW and LW also slightly decreased at the butt and slightly increased at the upper heights towards the bark (Luostarinen 2011a). Intra-ring density variation has been observed to decrease from pith to bark at 1.8 m height also in hybrid larch (Fujimoto et al. 2008). The reason for this may be differences in the accumulation of cell wall material into EW and LW and lignification of EW and LW, which are affected by ascorbic acid (Antonova et al. 2005), between the butt and the upper heights. An indicator of this may be the unexpected negative ratios between RD and 2CWT at the butt. Ascorbic acid and its oxidized form dehydroascorbic acid accelerate cell division and cell enlargement in EW, in which the lignification starts gradually, while during the LW development the concentrations decrease, and lignification of LW tracheids is at its highest at the beginning of their development. In addition, concentration of ascorbic acid, high in early stage of xylem development in growing season, correlate positively with radial enlargement of tracheids (Antonova et al. 2005), and cell senescence may start earlier at the butt than upper heights in the trunk (Kärkkäinen 1978), also possibly affecting 2CWT, as senescence decreases the lengthening of cambial initials (Bannan 1967). Furthermore, environmental factors such as temperature and precipitation, and date of snow melt have an impact on 2CWT, as radial cell enlargement and cell wall thickening have different temperature optima, for former it being higher, high precipitation increases cell wall thickness (Antonova and Stasova 1997), and late snow melt delays cambial activity (Kirdyanov et al. 2003); these factors may contribute differently to cell formation at different heights.

In conclusion, the observed radial variations for RD and 2CWT in this study were mainly what would be expected. However, the axial radial variation was different between the butt and other heights, which may be due to the negative ratios between RD and 2CWT at the butt. As the differences in 2CWT between EW and LW were smaller at the butt than the upper parts of the trunk, resulting the observed smallest density variation between EW and LW at butt height (Luostarinen

2011a), the wood of butt log is more homogenous than the wood of upper heights and is thus more suitable for structural purposes. Homogeneity of wood structure in structural uses can be kept as a good property, because as a consequence of it, other properties, e.g. mechanical ones, can be better predicted, and processing of wood is easier and working faces become smoother.

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