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Dendrochronologia 23 (2005) 93–104
DENDROCHRONOLOGIA
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ORIGINAL ARTICLE

Variations in the tree-ring structure of Norway spruce (*Picea abies*) under contrasting climates

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Received 10 July 2005; accepted 20 September 2005

Abstract

Variations in tree-ring structure from pith to bark of mature Norway spruce (*Picea abies* Karst. (L)) grown under contrasting climate conditions (warm-dry vs. cool-humid) in south-western Germany were investigated. Sample trees were from even-aged stands where no intensive silvicultural treatments had taken place. The cell number (CN), diameter (CD), lumen diameter (CL) and wall thickness (CW) were measured from stem cross-sections taken at breast height. A raw data chronology of each cell parameter was established for the whole annual ring (AR), earlywood (EW), latewood (LW), and transition wood (TW). The long-term trends of the cell parameters were generally non-linear, parameter-specific in AR and EW and similar over sites. Those in LW were site-specific and similar over cell parameters. The variation of the same parameter, expressed by the coefficient of variance (CV), tended to increase from EW towards LW and was clearly higher for CN than for other cell parameters of all tree-ring zones. Trees from the warm-dry site had more LW cells and substantially thicker CW, whereas those from the cool-humid site had larger EW cells. These observed differences are likely due to the hydraulic adaptation mechanisms of trees to different site conditions.

Keywords: Tree-ring structure; Long-term trend; Climate conditions; Growth adaptation

Introduction

Morphologically, the tree ring of conifers consists roughly of two groups of cells, called earlywood (EW) and latewood (LW) cells. The large EW cells mainly support water transport from roots to leaves, whereas LW cells rather contribute to mechanical support (Creber and Chaloner, 1990). The general trend of cell characteristics such as the number, size, and wall thickness from pith outwards is well understood. More than a century ago, Sanio (1872) suggested five laws on cell growth for Scots pine. Since then, it has been repeatedly observed that the cell size consistently follows Sanio's law; it increases with tree age but remains constant after reaching a certain dimension (Vysotskaya and Vaganov, 1989; Lindstrom, 1997; Mencuccini et al., 1997; Spicer and Gartner, 2001). Cell number (CN) generally declines with age, whereas cell wall thickness (CW) increases (Larson, 1963; Mitchell and Denne, 1997; Wimmer, 2002). Juvenile wood generally has smaller cells, thinner cell walls, and a lower density than mature wood (Zobel and van Buijtenen, 1989).

Besides the trends related to tree age, environmental influences on tree-ring structure are evident. Cell size is

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doi:10.1016/j.dendro.2005.09.002

influenced largely by the availability of water. It has been repeatedly observed that water-stressed trees have smaller cell conduits in comparison with non-stressed ones (von Wilpert, 1991; Dünisch and Bauch, 1994; Abe et al., 2003). A decrease in cell size is also reported along altitudinal gradients (Mayr et al., 2002). Gindl et al. (2001) found that a tree at high altitude had thinner cell walls, but a higher lignin content, whereas one at low altitude had thicker cell walls and experienced a longer lignification process. Unusually low temperatures during the growing season are also often related to thinner cell walls (Yamaguchi et al., 1993; Gindl and Grabner, 2000; Wang et al., 2002).

However, many questions are still open. Little is known yet whether systematic differences exist in trends for cell characteristics in the same tree ring depending on different tree-ring zones. Do different site conditions have any influence on such changes? If yes, are they constant throughout the various tree-ring zones? Numerous studies on hydraulic architecture have revealed an interesting systematic change in cell lumen size depending on site conditions. However, what about other cell parameters in the same tree ring? Furthermore, how do the structural differences observed in different environments develop over time? Is it constant during the lifetime of trees?

We have explored these questions by analyzing the tree-ring structure from pith to bark of mature Norway spruce (*Picea abies* (L.) Karst.) growing in warm-dry and cool-humid climates. The objectives of this study were (1) to quantify the variability of cell parameter chronologies, (2) to quantify their long-term trend variances, (3) to depict the pattern of the long-term trend, and (4) to examine the dependency of these aspects on different intra-ring zones, individuals and sites.

Material and methods

Study sites

The study sites were chosen from the most contrasting climate conditions in south-western Germany (Fig. 1). The Schluchsee site is located on the NE side of an upper slope in the southern Black Forest (47° 49′ N, 8° 06′E, 1202 m a.s.l.). It belongs to the "Feldberggebiet", a natural habitat for Norway spruce (Schmidt-Vogt, 1977). The climate here is cool and humid. The mean monthly temperature *in situ* from 1988 to 1994 ranged from −2.3 °C in December to 13.3 °C in July; the annual mean is 4.5 °C. The annual precipitation is, on average, 1803 mm; about 42% of it are falling during the May–October period (Raspe et al., 1998). Although the forest soil is a podsolized, sandy loam developed from base-poor granite, the availability of soil nutrients can be generally noted as "good", particularly owing to high soil microbial activity (Raspe et al., 1998).

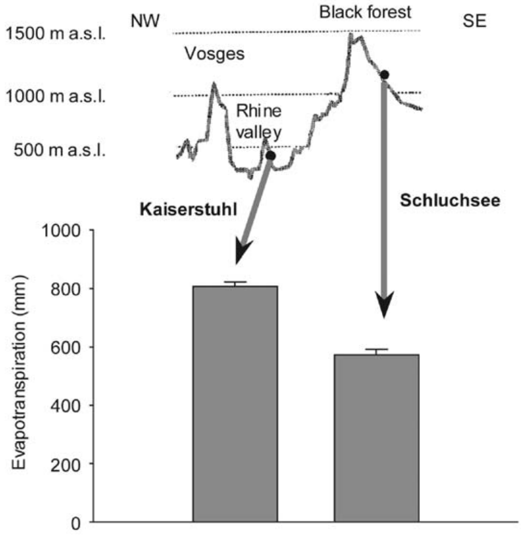

Fig. 1. Vertical profile (top) and mean annual evapotranspiration with standard error (bottom) of the study sites. Evapotranspiration was estimated using the Haude equation for the time period 1988–1995. For the Schluchsee site, climate records were measured on the study site. For the Kaiserstuhl site, climate records from DWD station Vogtsburg-Oberrotweil (Deutscher WetterDienst: ID 2305), situated about 5 km from the study site, were used.

The Kaiserstuhl site is located on the SE side of a hilly Rhine valley (48° 07′ N, 7° 67′ E, 260 m a.s.l), in one of the warmest and driest regions of Germany (Vogel, 1964), just about 40 km north-west from the Schluchsee site, but almost 1000 m lower (Fig. 1). According to records from the nearest Deutscher WetterDienst (DWD) station Vogtsburg-Oberrotweil (ID 2305), the mean temperature in the coldest month (December) was 3.4 °C between 1988 and 1995, and reached a maximum of 20.5 °C in July; the annual mean is 11.1 °C. The annual precipitation is only 649 mm, less than half that of the Schluchsee site. However about 62% of it are falling during the May–October period. This warm, dry climate is directly related to a high atmospheric evaporative demand, as represented in Fig. 1. The forest soil is a very rich and fertile loess with a high water-holding capacity. Under this warm climate regime, Norway spruce grows only in patches on the foothills that are poorly exposed to the sun (Veres, 1975; Vogel, 1964). On both sites, Norway spruce grows in even-aged stands and no intensive silvicultural activities have been reported.

Table 1. Mensuration characteristics of sample trees on Schluchsee and Kaiserstuhl site

Site	Tree no.	Age at 1.3 m	Diameter at 1.3 m (cm)	Height (m)	H/d value (%)	Mean radial increment (mm)
Kaiserstuhl	K1	86	73.3	34	46	3.35 (3.57)[a]
	K2	89	67.5	36	54	3.43 (3.63)[a]
	K3	94	50.3	32	63	2.38 (2.61)[a]
	Mean	90	63.7	34 (29)[a]	54	3.05 (3.27)[a]
Schluchsee	S1	62	43.3	24	56	3.15
	S2	58	43.4	27	62	3.41
	S3	60	34.9	25	79	2.66
	Mean	60	40.5	25	66	3.07

[a] Values within parentheses indicate the average height of Kaiserstuhl trees at the age of 60 years, which is reconstructed by stem analysis in order to enable direct comparison with Schluchsee trees.

Selection of sample trees

Five trees were randomly selected from among the dominant trees at each site with the restriction that they have a conical crown without visible damage or abnormality on either the stem or the crown. These trees were harvested after the end of the growing season in 1992 at Schluchsee and in 1995 at Kaiserstuhl. In the field, the height and diameter at breast height (DBH) and the length of the inter-knots of each tree were measured. Because of the enormous time expenditure necessary for the measurements, only three trees – the smallest and the two largest – were used for this study. The sample trees in Kaiserstuhl were on average 30 years older and had a lower *h*/*d* ratio than the Schluchsee trees; however, when compared at the same age, they were about 4 m higher (see value in parentheses in Table 1). By contrast, the annual radial growth was similar, even though the Kaiserstuhl trees had a slightly higher growth rate (Table 1).

Radial increments and cell measurement

A stem cross-section was taken at breast height (1.3 m) from each sample tree, air-dried at ambient temperature for several months, and then sanded with a belt sander. The annual radial increment (RI) was measured to the nearest 0.01 mm along eight equidistant radii beginning from the north, and then cross-dated (Stokes and Smiley, 1968). After the measurement, an approximately 10 cm-wide segment was removed from two radii of each cross-section; from the north side for all sample trees, and from the south side for all Kaiserstuhl trees, and from the south-east (S1), east (S3), and south-west (S5) sides for the Schluchsee trees. The sanded wood surface was removed using a circular saw machine, and smoothed by an ultra-precise milling machine. Images were taken every 200 μm from pith to bark with a B/W-CCD camera (C-mount: Sony, Tokyo, Japan) attached to a reflected-light microscope (Axiotech$^{\mathrm{vario}}$ 25HD: Zeiss, Jena, Germany) with an objective of 50 × magnification. The resolution of the images was 0.358 μm/pixel. The images were spliced for each tree ring, then cell measurements were conducted in radial direction (for detailed information, see Spiecker et al., 2000). The cell parameters obtained were the number (CN), diameter (CD), lumen diameter (CL), and wall thickness (CW) of each tracheid along the selected radial cell files. In general, four cell rows per tree ring were measured for each radius, each cell row contained of a continuous sequence of relatively large cells that crossed the entire tree ring, and each cell row was located away from resin ducts. In the juvenile wood, however, it was difficult to find cell files which met these criteria. Therefore, two radial cell files were chosen, depending on the radius, up to the eighth ring. Thus, in total, four or eight cell files for each tree ring were included in the analysis. The present study is based on 323423 cells from 441 tree rings: 178 tree rings (1931–1992) from Schluchsee and 263 tree rings (1904–1995) from Kaiserstuhl.

Data preparation

Because of the smooth transition from EW to LW in Norway spruce (Schweingruber, 1990, also see Fig. 2), we grouped the cells of each tree ring into three intra-ring zones, namely EW, LW, and transition wood (TW) (Park, 2000). The EW/LW demarcation is generally based on the wall–lumen relation of the cells. Mork's definition (1928) has long been in wood anatomy (Denne, 1988). Mork suggested dividing a tree ring at the position where 2 × double CW exceeds the CL, in other words, the index value (= 2 × double CW/CL × 100) exceeds a threshold value of 100 (Fig. 2). The EW was, in this study, further divided by a threshold value of 50 (Fig. 2). Raw-data chronologies were then established for the whole annual ring (AR), as well as for these three intra-ring zones.

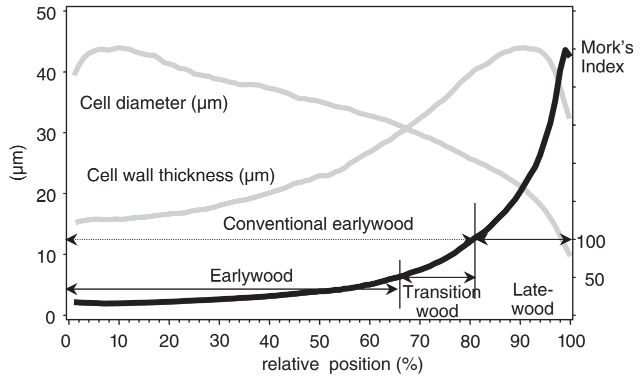

Fig. 2. Intra-ring demarcation with mean curves of cell diameter and cell wall thickness, based on data of 322424 tracheids in 441 tree rings from the study sites. The mean curves were made by using biweight mean in order to avoid the influence of outliers. For a better presentation the cell wall thickness was multiplied by 5.

Statistical analysis

We used the biweight mean for establishing each chronology as well as the intra-ring profile of the ring characteristics in order to avoid any possible influence of outliers as well as of non-normal data distribution (see Hoaglin et al., 1983; Cook et al., 1990). The data structure of each tree was then summarized as box-whisker plot for a growth-level comparison. The time-related variability of each chronology was determined by the coefficient of variance (CV), allowing a direct comparison of variables of different scales and magnitudes. The long-term trends in the chronologies were estimated using the locally weighted polynomial regression (LOESS) suggested by Cleveland (1979). LOESS is one of the flexible non-parametric methods that are suitable for modeling complex processes for which no theoretical model exists. For each data point, a subset of data is determined, then a polynomial (local fit) is fitted using weighted least squares. This gives more weight to points near the point whose response is being estimated and less weight to points further away. The value for a given data point is then obtained from this local polynomial model. The trend line (LOESS fit) is established by joining the obtained points after regression function values have been computed for each of the data points. In this study, the first order polynomial (linear) with a tri-cub weight function was used for local fit. The smoothness or flexibility of the LOESS function is dependent on the sample size of the subset (K). It is controlled by the smoothing parameter α, which varies between $(d+1)/n$ and 1, with d denoting the degree of the local polynomial. In this study, α was 0.34 and 0.5 for Kaiserstuhl and Schluchsee trees, respectively, in order to assure that the K was equal for all sample trees (about 30 years). Although K is determined by a nearest neighbors algorithm, since our data were distributed evenly through the X-axis (cambial age) and had no missing value, the LOESS fit worked as a fixed bandwidth. The long-term trend was defined as the LOESS fit estimated with about 30 years of subset data. All data handling and statistical analyses were done with Statistical Analysis Software (SAS, Ver. 8.01 SAS Institute, Cary, NC, USA).

Results

Long-term trend and variance of radial increment

The RI of all six sample trees increased rapidly in their early life without any sign of suppression or disturbance (Fig. 3a). After about 20 years, the increment started to decline. There was no substantial difference in average growth between the sites (Fig. 3b). However, differences between individuals within the sites were large; extremely wide rings, containing compression wood, indicated by a longer whisker length and stars, were observed more commonly in the Kaiserstuhl trees.

Long-term trend and variance of cell parameters

The estimated long-term trends for each cell parameter are plotted in Fig. 4, the largest differences were found after the first 30 years. Therefore, box-whisker plots were made only for the period from 30 to 58 years (Fig. 5).

At the whole AR level, each cell parameter showed its own distinctive long-term trend and did not change substantially between the two sites. The CN for Kaiserstuhl trees, however, decreased more slowly than that for the Schluchsee trees so that they had slightly more cells with age. The CD and CL increased rapidly. After a certain tree age (the inflexion point) this tendency diminished or leveled off. The Schluchsee trees reached this point at about 30 years, 10 years later than the Kaiserstuhl trees. In consequence, the Schluchsee trees had larger cells after the first 20 years. The CW of the Kaiserstuhl trees increased more rapidly compared to those of Schluchsee trees so that they are about 30–100% thicker. This rapid increase diminished after 40–60 years.

Comparing intra-ring zones (EW, TW, LW), a cell parameter-specific difference was only evident in EW. As opposed to AR, the cell walls on both sites show a linear tendency to be thicker. There was no substantial difference between the sample sites for CN either, but two of the Kaiserstuhl trees (K1, K2) had smaller CD and CL than the others. Also, interesting to note was the distinctive ring structure of the K3 tree; it had markedly

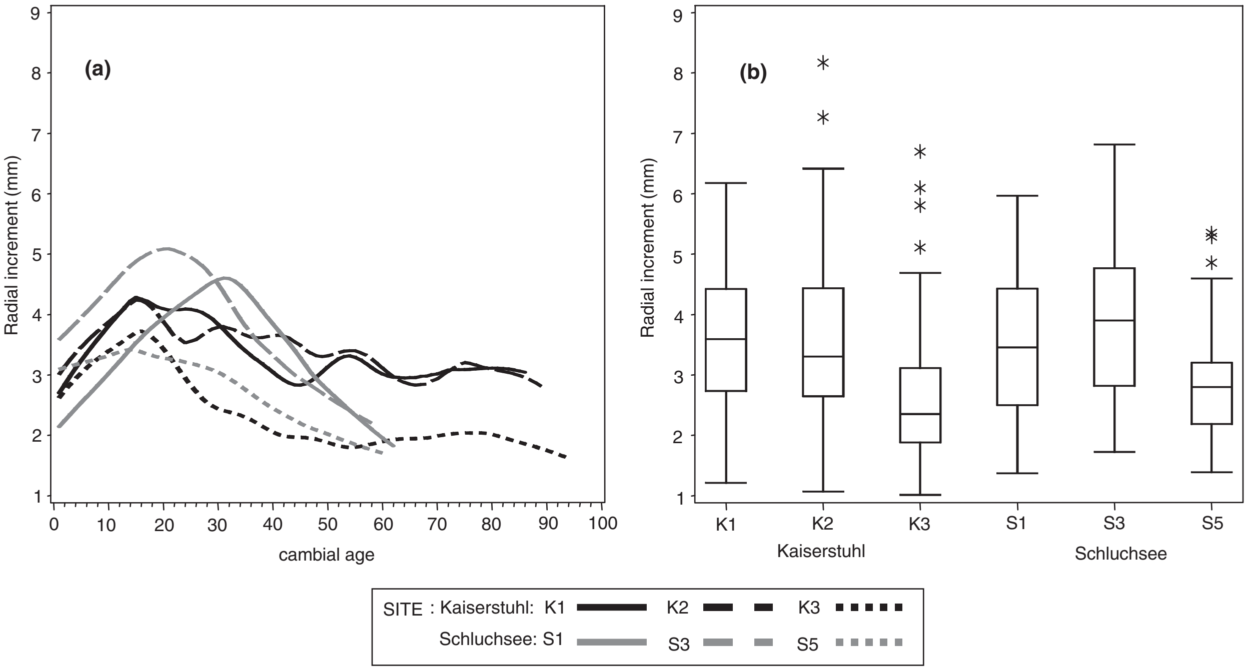

Fig. 3. Long-term trends (a) and box-whisker plots (b) of radial increment: long-term trend is estimated by LOESS function with $K =$ about 30 years. Box-whisker plots are made for the maximum common age period of the first 58 years. The horizontal lines inside the boxes represent the median. The top and bottom of the box represent the 3rd and the 1st quartile, respectively. The distance between these two is the interquartile range (IQR). Whiskers are drawn at the smallest and largest data point within 1.5 times of the IQR from the both sides of the box. The outliers are identified individually with stars.

fewer cells, but clearly thicker cell walls than other trees in EW and TW. Its CD and CL were almost of the same level as those from the Schluchsee trees for EW, and were even larger in TW.

Such a parameter-specific difference is not evident in the LW; all cell parameters from the same site showed a similar long-term trend and growth level. By contrast, the differences between the sites were clearly recognizable. All cell parameters of the Kaiserstuhl trees increased with tree age, but at an exponentially decreasing rate. On the other hand, those of Schluchsee trees only fluctuated, wave-like, around a constant level with age. Therefore, the difference in growth level at both sites became clearer after passing the culmination point of the first wave of the Schluchsee trees. There was no substantial difference for TW between both sites, either in growth level or in long-term trend, even though the CNs of the Schluchsee trees tended to decrease with tree age, whereas those of the Kaiserstuhl trees showed no substantial change.

Decomposition of variations in cell parameters

Table 2 lists the CV and the percentage of variance explained by the long-term trend. The CN clearly had a higher CV than all other cell parameters in a given tree-ring zone for both sites, and the CV of cell parameters tended to increase from EW towards LW, except for the CN which had the highest CV in TW. Cell parameters in AR generally had a lower CV than inter-ring zones (EW, TW, and LW), except for the CW in the Kaiserstuhl trees.

When comparing the CV in AR at the two sites, differences were small. However, the CV of CW in AR was almost twice as high in Kaiserstuhl as in Schluchsee. Schluchsee trees tended to have more variation in LW, whereas Kaiserstuhl trees varied more in TW. In EW, the CN and CW of Kaiserstuhl trees have a larger variation than those of Schluchsee trees, whereas the variation in CD and CL was larger in Schluchsee trees. The difference within the same parameters was very small.

On average, 67% and 51% of these variations were explained by the long-term variation for Kaiserstuhl and Schluchsee trees, respectively. As opposed to CV, the long-term variation of cell parameters was generally very large in EW and AR at both sites and tended to decrease from EW to LW, especially in Schluchsee site, e.g., it went from 79% to 7% for CL in the S3 tree (Table 2). The CW of the Kaiserstuhl trees showed, however, an opposite tendency and increased towards LW. The CD in EW and AR had the largest average long-term variation at both sites (up to 92%), whereas the CN in TW for Kaiserstuhl trees had the smallest average variance explained by long-term variation (13%).

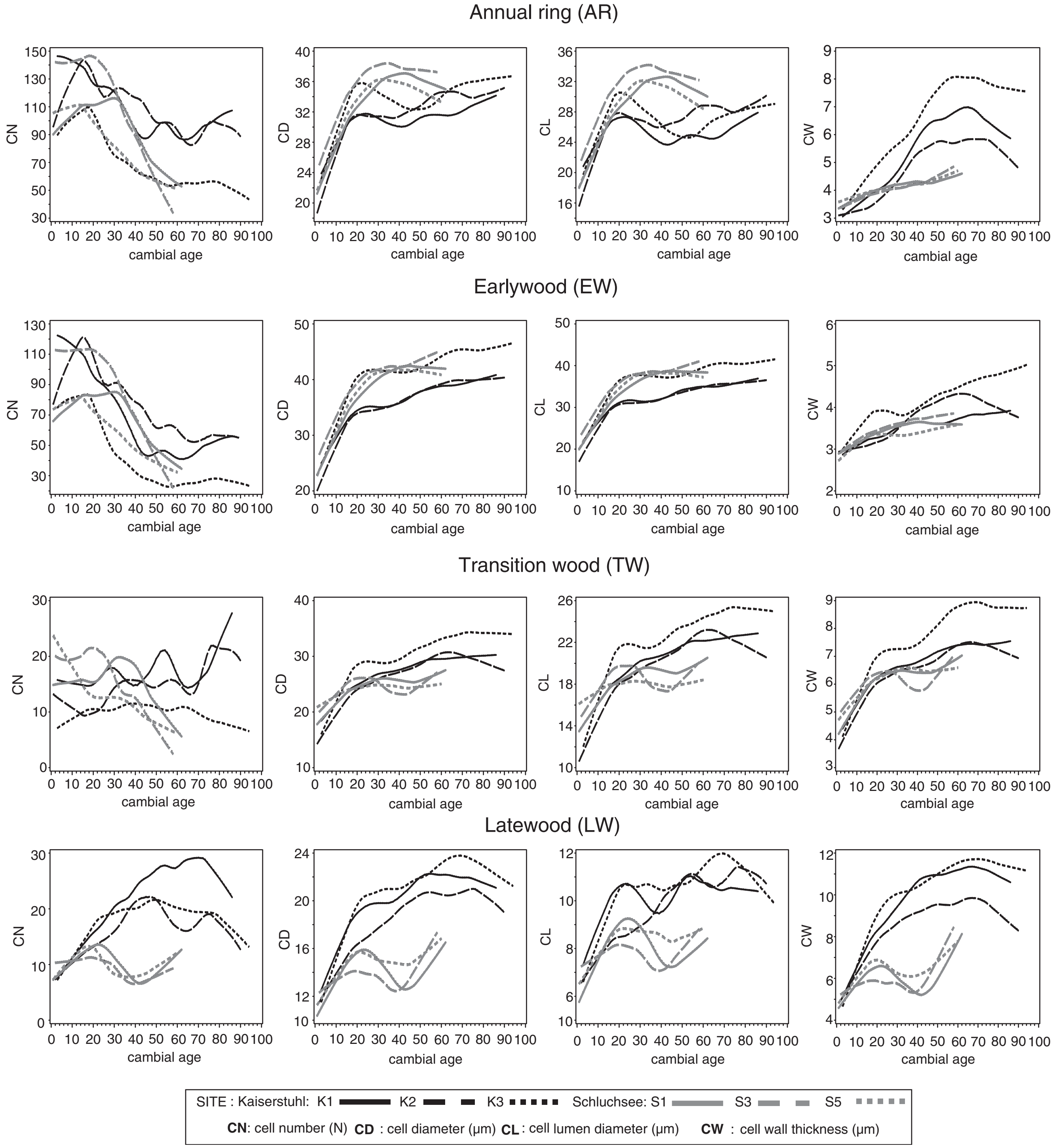

Fig. 4. Long-term trend of four cell parameters estimated with LOESS function. The LOESS fit is made with $K =$ about 30 years for all cell parameters.

Discussion

Our results show that the long-term trends of each cell parameter are relatively similar between individuals for all tree-ring zones on the same site, even though the growth levels can vary considerably (Figs. 4 and 5). The pattern of total time-related variance between the cell parameters, expressed by CV, is very similar for both sites (Table 2). In line with previous studies, the CN shows the same type of variation as the RIs (Fritts et al., 1991; Little and Sundberg, 1991; Vaganov, 1996), and cell size and wall thickness tend to have lower variance

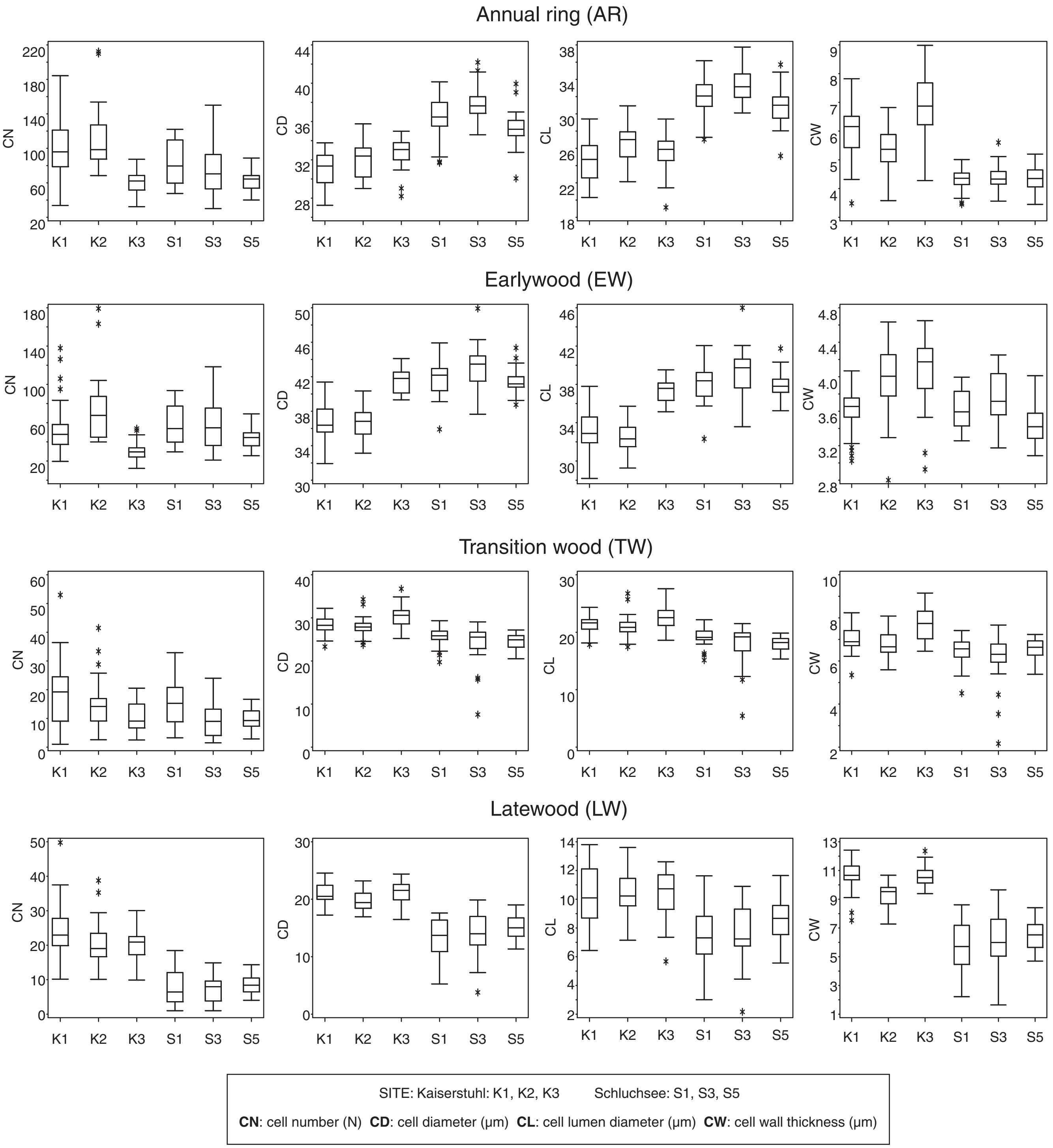

Fig. 5. Box-whisker plots of cell parameters for the period from 30 to 58 year. For the explanation on the plots, see in Fig. 3.

(Park and Telewski, 1992; Yasue et al., 2000). Through a detailed comparison (Table 2 and Fig. 4), the large long-term variances in EW, that explain up to 94% of individual variance (e.g., CD of the K2 tree), are seen to be rather parameter-specific; regardless of site, the same parameter shows a similar trend. However, the trend variance in LW should be site-specific, since it clearly differs between the sites, but is similar between cell parameters. These long-term variances have been considered as "noise" in the domain of dendroclimatology, since they are believed to be largely influenced by non-climatic factors. For this reason, numerous sophisticated statistical methods have been developed to filter it out (see Fritts, 1976; Cook and Kairiukstis, 1990). Our

Table 2. Coefficient of variance (CV) and the percentage of variance ($R^2 \times 100$) explained by the long-term trend

Site	Zone	Parameter	CV				Variance explained by long-term trend (%)			
			1	2	3	Mean	1	2	3	Mean
Kaiserstuhl	AR	CN	31	40	43	**38**	42	26	55	**41**
		CD	8	13	11	**11**	72	82	77	**77**
		CL	10	14	13	**12**	56	71	64	**64**
		CW	27	24	25	**25**	79	83	88	**83**
	EW	CN	51	50	73	**58**	70	42	63	**58**
		CD	15	11	13	**13**	89	94	92	**92**
		CL	15	12	13	**13**	87	92	91	**90**
		CW	15	12	15	**14**	43	82	70	**65**
	TW	CN	65	80	48	**64**	13	15	12	**13**
		CD	13	17	16	**15**	79	86	84	**83**
		CL	13	18	16	**16**	77	84	80	**80**
		CW	14	17	18	**16**	73	81	85	**80**
	LW	CN	42	40	31	**38**	50	45	44	**46**
		CD	15	16	16	**16**	68	80	78	**75**
		CL	18	20	18	**19**	26	54	41	**40**
		CW	20	17	19	**19**	82	78	90	**83**
	Mean		**23**	**25**	**24**	**24**	**63**	**68**	**70**	**67**
Schluchsee	AR	CN	33	41	39	**38**	57	75	54	**62**
		CD	15	12	14	**14**	85	76	77	**79**
		CL	16	13	16	**15**	81	72	73	**75**
		CW	11	13	11	**12**	47	53	39	**46**
	EW	CN	43	37	48	**43**	54	76	41	**57**
		CD	14	16	16	**15**	91	79	89	**86**
		CL	15	17	17	**16**	91	79	89	**86**
		CW	10	9	9	**9**	51	54	56	**54**
	TW	CN	48	74	52	**58**	36	33	50	**40**
		CD	13	16	8	**12**	63	26	37	**42**
		CL	13	16	7	**12**	61	25	22	**36**
		CW	14	16	11	**14**	63	29	59	**50**
	LW	CN	49	56	46	**50**	34	14	32	**27**
		CD	23	26	17	**22**	33	14	26	**24**
		CL	25	27	18	**23**	29	7	17	**18**
		CW	26	28	18	**24**	34	26	35	**32**
	Mean		**23**	**26**	**22**	**24**	**57**	**46**	**50**	**51**

AR, annual ring; EW, earlywood; TW, transition wood; LW, latewood.

CN, cell number; CD, cell diameter; CL, cell lumen diameter; CW, cell wall thickness.

Data is listed in order of sample tree number (1, 2, 3): K1, K2, K3 for Kaiserstuhl, and S1, S3, S5 for Schluchsee. Long-term trend is estimated by using LOESS function with $K =$ about 30 years for all cell parameters.

study shows that this may be especially justified for EW cell parameters, since their total variance is largely explained by the trend variance and that is similar for the different sites. On the other hand, the long-term trend in LW shows interesting environmental "signals", even though they may not be exactly the same signals desired by dendroclimatologists since they do not fluctuate concurrently with the annual changes in climate parameters. In this context, high variability, expressed by a high CV value as well as a high proportion of short-term variation of LW cell parameters of the Schluchsee trees (see Table 2), may be particularly interesting for dendroclimatological study (see Mäkinen et al., 2002).

Although the RIs as well as the CN at both sites are comparable, though slightly higher for the Kaiserstuhl trees, they show a clear difference in cell morphology. The Schluchsee trees, grown in a cool and humid

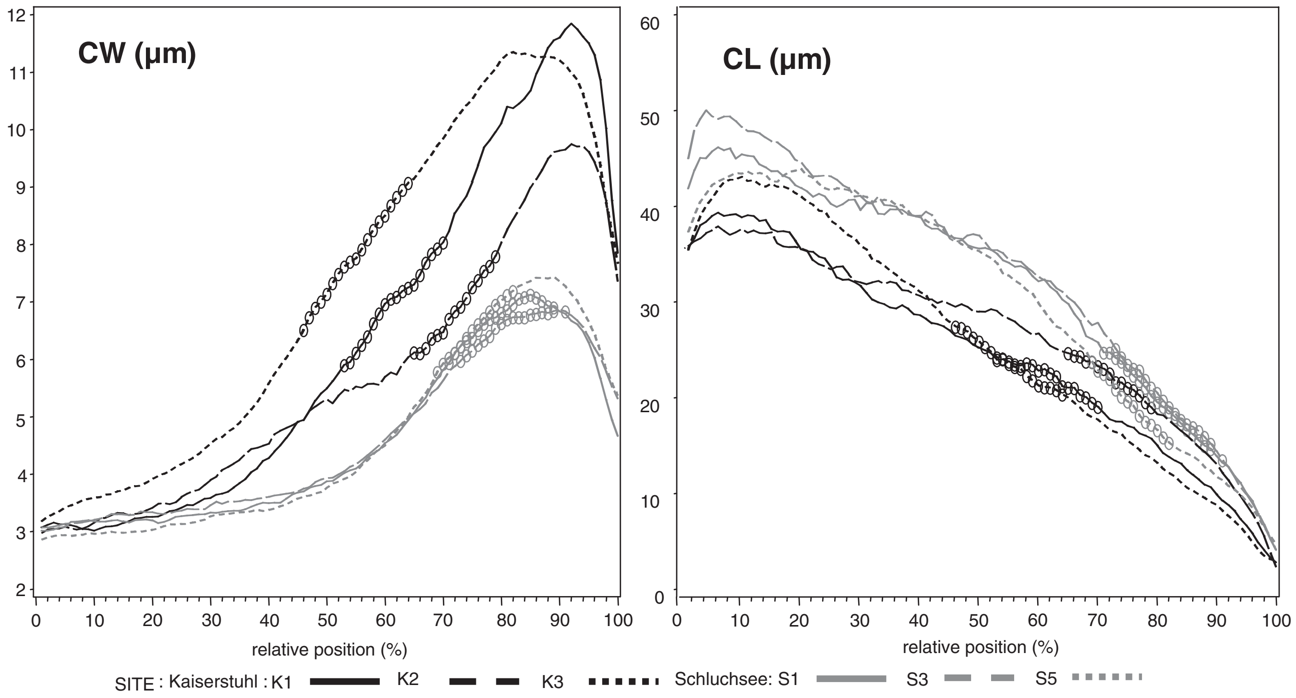

Fig. 6. Intra-ring profile of cell wall thickness (CW) and lumen (CL). The relative position was calculated relative to the CN, so that the first cell of a radial cell file was set as 1% and the last one as 100% of the intra-ring position. The cell positions in between were interpolated linearly. Each point on the curves represents the mean value of the period from 30 to 58 year. The open circles on the curves represent the location of the transition wood; before the open circle is the earlywood zone and after that the latewood zone.

climate, have much larger cells, while the Kaiserstuhl trees, grown in a warm and dry climate, have substantially smaller cells but thicker cell walls, resulting in a higher proportion of LW cells (Fig. 5).

The large cell size in the K3 tree, similar to or even greater than the Schluchsee trees in EW and TW (see Figs. 4 and 5), may be attributed to the demarcation method. A comparison of the intra-annual profiles revealed that, although the K3 tree had larger cells than the K1 and K2 trees in the first half of the tree ring, it was only the first 20% of the relative position that reached the level of the S5 tree, the smallest of all the Schluchsee trees for the given relative position, but still at a slightly lower level (Fig. 6). In contrast, the cell walls of the K3 tree were generally thicker than all the other trees. Thus, the K3 tree's smaller cell lumen, but thicker cell wall, resulted in the markedly earlier establishment of TW as well as LW; TW began at 46% of the relative position in the K3 tree, and LW began at 65%, whereas TW in the Schluchsee trees had not yet begun at that position. This gives the K3 tree the similar, and even greater average cell size compared to the Schluchsee trees for EW and TW, despite its smaller cells when compared at the same relative position. In the same light, it also explains why the Kaiserstuhl trees have larger LW cells than Schluchsee trees.

However, our findings for the Kaiserstuhl trees are inconsistent with the literature on tree hydraulic architecture, considering that the Kaiserstuhl site is located at much lower altitude than the Schluchsee site; Mayr et al. (2002) observed a decreasing cross-sectional area of Norway spruce tracheids along an altitude gradient from 800 to 1600 m in the Central Alps. According to Pittermann and Sperry (2003), narrowing cell size may be a protection mechanism of trees against freezing-induced embolism in cold climates. In this context, the altitude difference, and its correspondingly colder temperature, may not be a direct factor which characterizes the xylem structure of our sample trees.

Norway spruce places a high demand on water supply, whereas it is not especially sensitive to temperature (Schmidt-Vogt, 1977). According to Nebe's theory (1968), who defined the minimum existence for this tree species in western Europe on the basis of the average total precipitation from May to August, the Kaiserstuhl site is climatically close to the lower limit of existence. Presumably, the highly fertile loess soil assures a large water-holding capacity and a higher site productivity as indicated by the better height growth of Kaiserstuhl trees for a given age (Table 1). However, the extremely high summer temperature and low precipitation may not be favorable for Norway spruce. Numerous studies show that water-stressed plants have a smaller conduit size (e.g., von Wilpert, 1991; Dünisch and Bauch, 1994; Abe et al., 2003). The smaller cell size of Kaiserstuhl trees should be regarded in the context of growth-water relations. This is in disagreement with Maherali and DeLucia (2000), who reported larger cell lumens and an associated higher specific conductance in desert ponderosa pine compared to high mountain ponderosa pine. It is not clear whether this is due to a different adaptation mechanism for the different tree species and/or to the particularity of site conditions. Further studies on this subject are needed.

According to the cohesion–tension theory, water uptake in vascular plants occurs under negative pressure, regulated by transpiration through stomatal activity and leaf area adjustment. A major driving force is the atmospheric evaporative demand. However, extremely negative pressure can cause, in turn, a hydraulic failure by inducing cavitation and associated embolism (for a recent review on this subject refer to Cruiziat et al., 2002; Sperry et al., 2002). Even though we did not measure hydraulic parameters, the high evaporative demand at the Kaiserstuhl site, expressed by higher potential evaportranspiration (Fig. 1), may cause a more negative pressure in the tree stem, so that Kaiserstuhl trees may need to develop a more solid and resistant xylem structure in order to prevent possible catastrophic hydraulic failure. This hypothesis is supported by Hacke et al. (2001), who reported a positive relationship between wood density, correspondingly thicker cell walls, and resistance to cavitation. The authors suggested that this is for the maintenance of a safety factor against implosion of tracheids by negative pressure. The high amount of compression wood in Kaiserstuhl trees may also be understood in the same way, since the compression wood could provide more resistance to embolism in severe drought conditions, even though it is generally more vulnerable at high water potential (see Domec and Gartner, 2002). Maherali et al. (2004) also reported that cavitation resistance in conifers increased with decreasing mean annual precipitation. Furthermore, the high LW ratio in the Kaiserstuhl trees also may offer a higher safety margin against water loss due to its higher water storage capacity (Domec and Gartner, 2002).

On the other hand, Sellin (2001) observed in 30–50-year-old Norway spruce trees that the xylem is efficient for water transport and the stomata are more sensitive to atmospheric evaporative demand in trees subject to favorable growth conditions. According to Hagen–Poiseuille's law, the CL is the primary factor that determines xylem hydraulic conductivity for conifers (Zimmermann, 1983). Lancashire and Ennos (2002) have recently suggested in their model approach that a CL of 53 μm may be the "ideal tracheid diameter" for 3.97 mm of tracheid length, which maximizes its efficiency for water transport in terms of pore density and cell dimension. Interestingly, the size of the first-formed cells of the Schluchsee trees reaches almost this 'ideal cell size' (Fig. 6). The high EW ratio (Fig. 6) also indicates the effective water use of these Schluchsee trees, as supported by Domec and Gartner (2002), who observed that EWs specific conductivity was about 11 times higher than LWs in the tree rings of 21-old Douglas fir trees.

The dependency of this difference in tree-ring structure on tree age is also evident. The conductivity of trees generally increases with age. When compared with juvenile xylem, the mature xylem tends to have a higher water-transport capacity (e.g., Mencuccini et al., 1997; Spicer and Gartner, 2001; Domec and Gartner, 2003). The juvenile wood is generally defined as having a smaller cell size and a lower density with a high variability, while the structure of mature wood is more stable (Zobel and van Buijtenen, 1989). In this context, it appears that the Kaiserstuhl trees reached their stable cell size in EW much earlier than the Schluchsee trees (Fig. 4). Despite the smaller initial size, the rapidly increasing CW of Kaiserstuhl trees also indicates that these trees have achieved and reinforced their drought-resistant xylem structure with time.

Conclusion

The comparison of the tree-ring structure of Norway spruce from contrasting climates reveals that the long-term trend of cell parameters changes depending on intra-ring zone and can be modified by different site conditions, mainly those regulated by climate. They change in the way that all cell parameters in EW as well as AR have their proper, own distinctive pattern, which seems to change very little from site to site. Those in LW, however, were more influenced by site conditions. The influence of site conditions appears to intensify after the first rapid growth of cell parameters.

Even though hydraulic measurements were not conducted on the sample trees, all structural evidence suggests that the Schluchsee trees, in a favorable climate, tended to maximize their water use by increasing tracheid diameter throughout their lifetime. In contrast, the Kaiserstuhl trees, in their unfavorable climate with high evaporative demand, developed a more drought-resistant structure that allowed a rather conservative use of water through increasing internal resistance by narrowing of the cell size and increasing wall thickness in order to prevent a possible catastrophic hydraulic failure.

However, because of limited material, our study should only be considered as a case study. The results may be valid only for trees which grow in comparable site conditions and are selected by using the same criteria. An extensive study using more material as well as proper statistical design would be needed for a generalization.

Acknowledgments

This study was funded by postgraduate scholarship (Landes-graduierten-förderungs-gesetz – LGFG) from the province Baden-Württemberg, Germany during 1996–1998 and partly by German Research Association (Deutsche Forschungs-gemeinschaft – DFG). The authors are grateful to Mr. F. Baab for preparation of samples and technical support.

References

Abe H, Nakai T, Utsumi Y, Kagawa A. Temporal water deficit and wood formation in *Cryptomeria japonica*. Tree Physiology 2003;23:859–63.

Cleveland WS. Robust locally weighted regression and smoothing scatterplots. Journal of American Statistical Association 1979;74:829–36.

Cook E, Kairiukstis A, editors. Methods of dendrochronology: applications in the environmental sciences. Dordrecht: Kluwer Academic Publishers; 1990 394pp.

Cook E, Shiyatov S, Mazepa V. Estimation of the mean chronology. In: Cook E, Kairiukstis A, editors. Methods of dendrochronology: applications in the environmental sciences. Dordrecht: Kluwer Academic Publishers; 1990. p. 123–32.

Creber GT, Chaloner WG. Environmental influences on cambial activity. In: Iqbal I, editor. The vascular cambium. New York: Wiley; 1990. p. 159–89.

Cruiziat P, Cochard H, Ameglio T. Hydraulic architecture of trees: main concepts and results. Annals of Forest Science 2002;59:723–52.

Denne MP. Definition of latewood according to Mork (1928). IAWA Bulletin 1988;10:59–62.

Domec J-C, Gartner BL. How do water transport and water storage differ in coniferous earlywood and latewood? Journal of Experimental Botany 2002;53:2369–79.

Domec J-C, Gartner BL. Relationship between growth rates and xylem hydraulic characteristics in young, mature and old-growth ponderosa pine tree. Plant Cell and Environment 2003;26:471–83.

Dünisch O, Bauch J. Influence of soil substrate and drought on wood formation of spruce (*Picea abies* [L.] Karst.) under controlled conditions. Holzforschung 1994;48:447–57.

Fritts HC. Tree rings and climate. San Diego: Academic Press; 1976. 255pp.

Fritts HC, Vaganov EA, Sviderskaya IV, Shashkin AV. Climatic variation and tree ring structure in conifers: empirical and mechanistic models of tree ring width, number of cells, cell size, cell wall thickness and wood density. Climate Research 1991;1:97–116.

Gindl W, Grabner M. Characteristics of spruce [*Picea abies* (L.) Karst] latewood formed under abnormally low temperatures. Holzforschung 2000;54:9–11.

Gindl W, Grabner M, Wimmer R. Effects of altitude on tracheid differentiation and lignification of Norway spruce. Canadian Journal of Botany 2001;79:815–21.

Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 2001;126:457–61.

Hoaglin DC, Mosteller F, Tukey JW. Understanding robust and exploratory data analysis. New York: Willey; 1983. 447pp.

Lancashire JR, Ennos AR. Modelling the hydrodynamic resistance of bordered pits. Journal of Experimental Botany 2002;53:1485–93.

Larson PR. Microscopic wood characteristics and their variations with tree growth. In: Proceedings of the IUFRO Section 41, September 11–13, Madison, WI, 1963. p. 1–24.

Lindstrom H. Fiber length, tracheid diameter, and latewood percentage in Norway spruce: development from pith outwards. Wood Fiber Science 1997;29:21–34.

Little CHA, Sundberg B. Tracheid production in response to indole-3-acetic acid varies with internode age in *Pinus sylvestris* stems. Trees 1991;5:101–6.

Maherali H, DeLucia EH. Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. Tree Physiology 2000;20:859–67.

Maherali H, Pockman WT, Jackson RB. Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 2004;85:2184–99.

Mäkinen H, Nojd P, Kahle HP, Neumann U, Tveite B, Mielikäinen K, et al. Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. Forest Ecology and Management 2002;171:243–59.

Mayr S, Wolfschwenger M, Bauer H. Winter-drought induced embolism in Norway spruce (*Picea abies*) at the Alpine timberline. Physiologia Plantarum 2002;115:74–80.

Mencuccini M, Grace J, Fioravanti M. Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. Tree Physiology 1997;17: 105–13.

Mitchell MD, Denne MP. Variation in density of *Picea sitchensis* in relation to within-tree trends in tracheid diameter and wall thickness. Forestry 1997;70:47–60.

Mork E. Die Qualität des Fichtenholzes unter besonderer Rücksichtnahme auf Schleif- und Papierholz. Der Papier-Fabrikant 1928;48:741–7.

Nebe W. Über Beziehungen zwischen Klima und Wachstum der Fichte (*Picea abies*) in ihrem europäischen Verbreitungsgebiet. Archive Forstwesens 1968;17:1219–38.

Park YI. Zur Auswirkung von Umwelteinflüssen auf das Wachstum von Fichten (*Picea abies* (L.) Karst.) auf der Grundlage bildanalytischer Verfahren zur Quantifizierung der Zellstruktur an Holzquerschnittsflächen (vol. 8). Freiburg iBr., Germany: Schriftenreihe Freiburg Forstliche Forschung (FFF); 2000. 193pp.

Park WK, Telewski FW. Anatomical parameters for dendrochronology: an image analysis of ponderosa pine from southeastern Arizona, USA. In: Rojo JP, Aday JU, Barlie ER, Araral RK, America WME, editors. Proceedings of the second Pacific regional wood anatomy conference, Laguna, Philippines, 1992. p. 301–20.

Pittermann J, Sperry J. Tracheid diameter is the key trait determining the extent of freezing-induced embolism in conifers. Tree Physiology 2003;23:907–14.

Raspe S, Feger KH, Zöttl HWE, editors. Ökosystemforschung im Schwarzwald: Auswirkungen von atmogenen Einträgen und Restabilisierungsmaßnahmen auf den Wasser- und Stoffhaushalt von Fichtenwäldern. Verbundprojekt ARINUS. Landsberg: Ecomed; 1998 533pp.

Sanio K. Über die Grösse der Holzzellen bei der gemeinen Kiefer (*Pinus sylvestris* L.). Jahrbücher für wissenschaftliche Botanik 1872;8:401–20.

Schmidt-Vogt H. Die Fichte; Taxonomie, Verbreitung, Morphologie, Ökologie, Waldgesellschaften (Band: 1). Hamburg Berlin: Paul Parey; 1977. 647pp.

Schweingruber FH. Mikroskopische Holzanantomie. Birmensdorf: WSL; 1990. 226pp.

Sellin A. Hydraulic and stomatal adjustment of Norway spruce trees to environmental stress. Tree Physiology 2001;21:879–88.

Sperry JS, Hacke UG, Oren R, Comstock JP. Water deficits and hydraulic limits to leaf water supply. Plant Cell and Environment 2002;25:251–63.

Spicer R, Gartner BL. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. Trees 2001;15:222–9.

Spiecker H, Schinker MG, Hansen J, Park YI, Ebding T, Döll W. Cell structure in tree rings: novel methods for preparation and image analysis of large cross sections for statistical evaluation of cell parameters of various tree species. IAWA Journal 2000;21:361–73.

Stokes MA, Smiley TL. An introduction to tree-ring dating. Chicago: University of Chicago Press; 1968. 73pp.

Vaganov EA. Analysis of seasonal tree-ring formation and modeling in dendrochronology. In: Dean JS, Meko DM, Swetnam TW, editors. Tree-rings environment and humanity. Proceedings of the international conference, Tucson, Arizona, 17–21 May. Radiocarbon 1996; 73–87.

Veres L. Erläuterungen zur Standortskarte Breisach und Kenzingen Kaiserstuhl. Freiburg i.Br.: Forstliche Versuchs -und Forschungsanstalt Abt. Botanik und Standortskunde; 1975. 65pp.

Vogel O. Zu den standörtlichen und waldbaulichen Verhältnissen im Kaiserstuhl. Allgemeine Forst- und Jagdzeitung 1964;135:162–71.

von Wilpert K. Intraannual variation of radial tracheid diameters as monitor of site specific water stress. Dendrochronologia 1991;9:95–113.

Vysotskaya LG, Vaganov EA. Components of the variability of radial cell size in tree rings of conifers. IAWA Bulletin 1989;10:417–28.

Wang L, Payette S, Bégin Y. Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec. Canadian Journal of Forest Research 2002;32:477–86.

Wimmer R. Wood anatomical features in tree-rings as indicators of environmental change. Dendrochronologia 2002;20:21–36.

Yamaguchi DK, Filion L, Savage M. Relationship of temperature and light ring formation at subarctic treeline and implications for climate reconstruction. Quaternary Research 1993;39:256–62.

Yasue K, Funada R, Kobayashi O, Ohtani J. The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors. Trees 2000;14:223–9.

Zimmermann MH. Xylem structure and the ascent of sap. Berlin: Springer; 1983. 143pp.

Zobel BJ, van Buijtenen JP. Wood variation: its causes and control. Berlin: Springer; 1989. 363pp.