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SCREENING VARIOUS VARIABLES OF CELLULAR ANATOMY OF SCOTS PINES IN SUBARCTIC FINLAND FOR CLIMATIC SIGNALS

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SUMMARY

This exploratory study on Scots pine in subarctic Finland was aimed at identifying the climatic signal(s) 'archived' in cellular anatomy and tree-ring variables, such as diameter and wall thickness of tracheids, or early- and latewood width, respectively. For this purpose, these variables were measured in increment cores year by year from 1961–2008 and compared to each other. According to the low values of some statistical descriptors (*e.g.*, expressed population signal and mean sensitivity) the cell-anatomical variables could, in fact, not be expected to be useful climatic proxies. Nevertheless, they turned out to significantly reflect other climatic signals than the tree-ring variables did. The tree-ring variables responded positively to temperature in July and August, whereas the cell-anatomical variables responded positively to temperature in December and January, prior to the growing season. These encouraging findings provide a strong rationale for further studies, and for enlarging the statistical sample size.

Key words: Subarctic Finland, Scots pine, cell anatomy, tree-ring structure, year-to-year variability, climatic influence.

INTRODUCTION

Annual variations in tree growth have proven to be a reliable natural proxy reflecting the year-to-year variability in regional climate conditions, such as temperature at high latitudes and altitudes (*e.g.*, Oberhuber *et al.* 2008; Tuovinen *et al.* 2008; Pisaric *et al.* 2009; Liang & Eckstein 2009) and precipitation in semi-arid and arid regions (*e.g.*, Diaz *et al.* 2001; Liu *et al.* 2003). Tree rings result from the total number of woody cells formed during a growing season (*e.g.*, Deslauriers & Morin 2005; Gričar *et al.* 2005; Fonti *et al.* 2010; Seo *et al.* 2011), and the width of the rings integrates all positive and negative influences, varying throughout the year of growth and even during prior years, into one measurable quantity (Fritts 1976).

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To obtain more environmental information than is possible from tree-ring width alone, anatomical features of woody cells and the signals 'archived' therein have been tentatively considered for more than half a century. But only by means of increasingly improved equipment and measuring techniques (*e.g.*, Eckstein *et al.* 1974; Vaganov & Terskov 1977; von Wilpert 1991; Spiecker *et al.* 2000; Gärtner & Nievergelt 2010) it has become possible to produce sufficiently large, statistically meaningful, sample sizes.

Most previous studies, however, have used deciduous tree species such as beech, oak or teak, and their vessel sizes as variable (*e.g.*, Woodcock 1989; Sass & Eckstein 1995; Pumijumnong & Park 1999; García-González & Fonti 2006; Tardif & Conciatori 2006).

Studies on conifers, in contrast, using different variables of cellular anatomy are less frequent (*e.g.*, Vaganov 1990; Deslauriers *et al.* 2008; Krause *et al.* 2010); few of them have considered the position of cells within a tree ring, that is, in the early- or latewood (*e.g.*, Eilmann *et al.* 2009) or in even narrower 'time-windows'. Such chronologically highly-resolved time series of cell-anatomical variables, however, have neither been systematically screened for their climate information nor been tested as to how many tangential rows of tracheids should be included to enhance the climatic signal.

The present study, therefore, was aimed at 1) establishing various chronologies of cellular anatomy in Scots pine in northern Finland, 2) screening them for their climatic signals, and 3) comparing these signals with those reflected by tree-ring widths.

MATERIAL AND METHODS

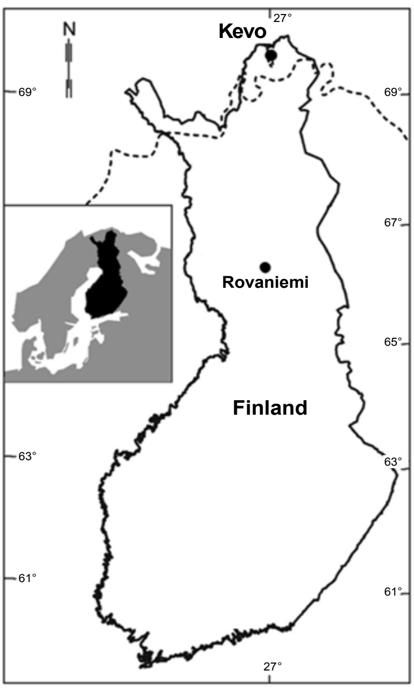

Figure 1. Study site near Kevo (69° 40' N; 27° 05'; 101 m asl) and the northern tree line of Scots pine (dashed line); the Arctic Circle goes through Rovaniemi.

Site and study trees

Our study site is located near Kevo (69° 45' N, 27° 01' E, 101 m asl) in northern Finland, approx. 60 km north of the contiguous Scots pine tree line, and part of the subarctic forest tundra vegetation zone (Fig. 1). Scots pine (*Pinus sylvestris* L.) and mountain birch (*Betula pubescens* subsp. *czerepanovii* (Orlova) Hämet-Ahti) are the dominant tree species (Kallio & Hurme 1983) this far north. We took one increment core each from ten dominant, over 100-year-old, Scots pine trees. Their average diameter at breast height and height were about 28 cm and 12.5 m, respectively.

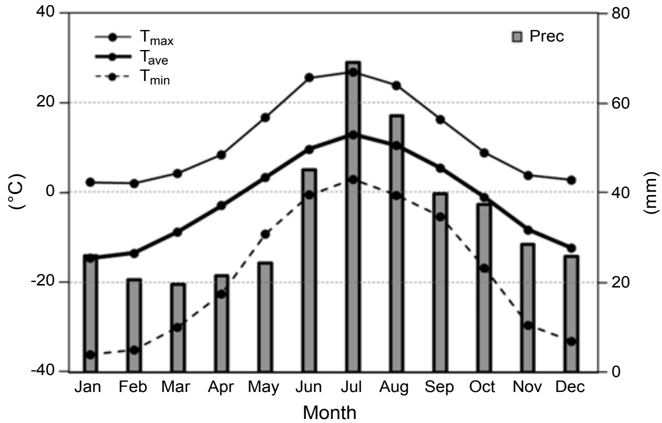

Figure 2. Monthly maximum (T_{max}), average (T_{ave}) and minimum (T_{min}) temperature and monthly sum of precipitation (Prec) at the study site (1962–2008) (Finnish Meteorological Institute).

Meteorological data at the study site

The local climate is characterized by an annual mean temperature of −1.6 °C, whereby the average temperatures of the coldest and warmest months, January and July, are −14.5 and +12.9 °C, respectively. The mean sum of the annual precipitation is 415 mm, with the lowest and highest values in March (19.7 mm) and July (69.0 mm), respectively (Fig. 2).

Monthly average (T_{ave}), maximum (T_{max}) and minimum (T_{min}) temperature data, as well as monthly sums of precipitation (Prec), were obtained from a weather station installed at the study site by the Finnish Meteorological Institute; the measurements started in 1962.

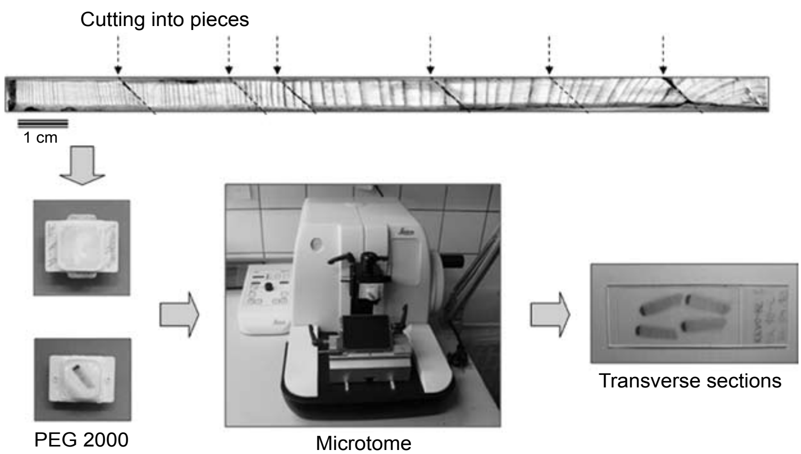

Figure 3. Sample preparation: obliquely dissecting an increment core in shorter pieces, embedding them into polyethylenglycol (PEG) 2000 and cutting transverse sections of 7–9 μm thickness by means of a rotary microtome.

Preparation of transverse sections from increment cores

First, all ten increment cores were used to measure the tree-ring widths (Aniol 1983). Then, the cores were divided into shorter pieces of ≤ 2.5 cm in length in order to fit in embedding forms filled with liquid polyethylene-glycol (PEG) 2000 (Fig. 3). These separating cuts were made obliquely, to enable a precise re-assembly of the image files into continuous time series, as described in the next paragraph. Then, 7–9-µm-thick cross sections were cut by means of a rotary microtome (Leica, RM2145) and stained with aqueous 1% safranin to enhance the contrast between cell walls and lumina. However, the cores from two trees were not suitable for cutting thin sections because of their soft consistency, so only eight trees remained for further analysis.

Measuring of cell-anatomical variables

Using a camera (AxioCam MRc, Carl Zeiss AG) installed on a light microscope (Axiovert25, Carl Zeiss AG) the transverse sections were converted into image files to measure various components of the tracheids, *viz*. lumen area (LA), cell-wall thickness (CW), lumen diameter (LD), and cell diameter (CD), all in the radial direction (Fig. 4), using WinCELL™ software (Régent Instruments Inc.). According to Rossi *et al*. (2006), these measurements were taken along three radial transects through each tree ring from 1961–2008; magnification was ×100. In order to determine how many tangential rows of tracheids in each tree ring should be taken into account to obtain a significant climatic signal, cell-anatomical variables were measured from the first 10, 30, and 50% of tangential tracheid rows in a tree ring, and from the entire earlywood (hereafter called ‘options‘); latewood was not considered due to the small number of tangential tracheid rows (5.7 ± 2.4) (see Table 1a). The attribution of the tracheids to early- or latewood, and hence the determination of the earlywood (EW) and latewood (LW) widths, was made using WinCELL™ software, following Mork’s formula (1928). Finally, the ratio between late- and earlywood widths (LE) was computed. All measurements were treated as time series.

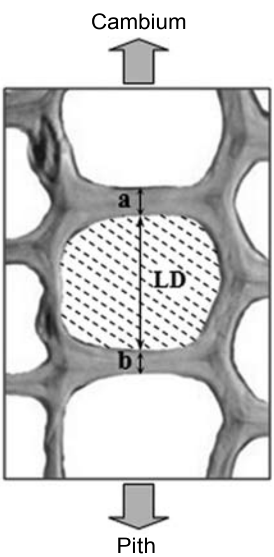

Figure 4. Definition of the cell-anatomical variables used: lumen area (hatched) (LA), lumen diameter (LD), cell-wall thickness (CW = a/2+b/2), cell diameter (CD = a/2+LD+b/2).

Standardization and chronology building

The tree-ring width and earlywood width time series of the individual study trees showed significantly high autocorrelations due to non-climatic age- and diameter-related low-frequency variability. Therefore, they had to be detrended using the ARSTAN program (Cook *et al*. 1990) by fitting a linear or negative exponential function to them, to obtain indexes of tree-ring width and earlywood width. Finally, a chronology was

Table 1. Tree-ring and cell-anatomical variables: a) tree-ring variables; b) cell-anatomical variables according to various grouping options.

a)

	Tree-ring width (mm)	Earlywood width (mm)	No.*	Latewood width (mm)	No.*	Ratio between late- and earlywood width
Ave	0.55	0.43	11.5	0.11	5.7	0.27
SD	0.19	0.16	4.2	0.05	2.4	0.12
CV	0.35	0.37	0.37	0.45	0.42	0.44

* Number of tangential rows of tracheids.

b)

Options	Cell-wall thickness (μm)			Cell diameter (μm)			Lumen diameter (μm)			Lumen area (μm)		
	Ave	SD	CV	Ave	SD	CV	Ave	SD	CV	Ave	SD	CV
10	2.97	0.42	0.14	37.43	3.91	0.10	31.49	3.73	0.12	969.24	161.80	0.17
30	2.98	0.39	0.13	38.70	3.09	0.08	32.75	2.94	0.09	1014.66	147.59	0.15
50	3.08	0.41	0.13	38.48	2.85	0.07	32.33	2.77	0.09	996.37	137.02	0.14
earlywood	3.22	0.39	0.12	37.22	2.71	0.07	30.78	2.45	0.08	939.31	133.33	0.14

Ave: average; SD: standard deviation; CV: coefficient of variance; *: % of total number of tangential rows of tracheids.

assembled for each of the four tree-ring variables. None of the four wood-anatomical variables showed any significant autocorrelations, so detrending was omitted. Before a chronology for them could be assembled, we had to decide for one of the four options; this was achieved according to the statistical descriptors, introduced in the next sub-chapter.

Statistical analyses

Each of the eight chronologies (four tree-ring related and four cell anatomy related variables) was characterized according to its expressed population signal (EPS) and signal-to-noise ratio (SNR) (Briffa & Jones 1990) to identify its reliable portion, the correlation between the trees (R_{bt}) to describe the average similarity between the time series considered for assembling a chronology, the mean sensitivity (MS) as an expression of the year-to-year variability, the first-order autocorrelation (R_{auto}) as a measure of the persistence of the time series, and the variance contained in the first eigenvector to obtain the common variance for the time series involved (Fritts 1976). In order to predict a strong dendroclimatological potential for a variable, all these descriptors, except R_{auto}, should be high.

All eight chronologies were correlated with each other and a correlation matrix was assembled. Furthermore, a factor analysis was performed using the option of VARIMAX orthogonal factor rotation (SAS 9.2) to reduce the number of the observed variables (in our case eight) to a smaller number of so-called unobserved variables or factors (Reise *et al*. 2000); to determine this number, the eigenvalue-greater-than-one rule was applied (Kaiser 1960).

The responses of the tree-ring and cell-anatomical chronologies to climate were calculated using Pearson's correlation coefficient (SAS 9.2) with monthly climate data from the prior September to the current August, between 1962 and 2008.

RESULTS

Basic tree-ring and cellular anatomy variables

The mean tree-ring width of the study trees was 0.55 ± 0.19 mm, of which 78 % was earlywood (Table 1). To adequately compare the range of variation of all eight variables, their standard deviation was normalized by dividing it through the mean value of the respective variable, resulting in the coefficient of variance (CV). According to the CVs, a distinctly higher year-to-year variability was shown for all tree-ring variables than for the cell-anatomical variables; at this point in time, this could be interpreted as inferiority of the cell anatomy variables compared to the tree-ring variables.

The graphical presentation of the raw measurements of the tree-ring and cell-anatomical variables makes the qualitative differences between both groups strikingly visible, in particular as regards the similarity among the time series per variable (Fig. 5).

For all tree-ring variables, the values of the statistical descriptors were – according to Briffa and Jones (1990) – in the usual order of magnitude (Table 2). But for all cell-anatomical variables, the values of the statistical descriptors were extremely low, but largest for the 50 % option. Therefore, we decided to assemble four cellular anatomy

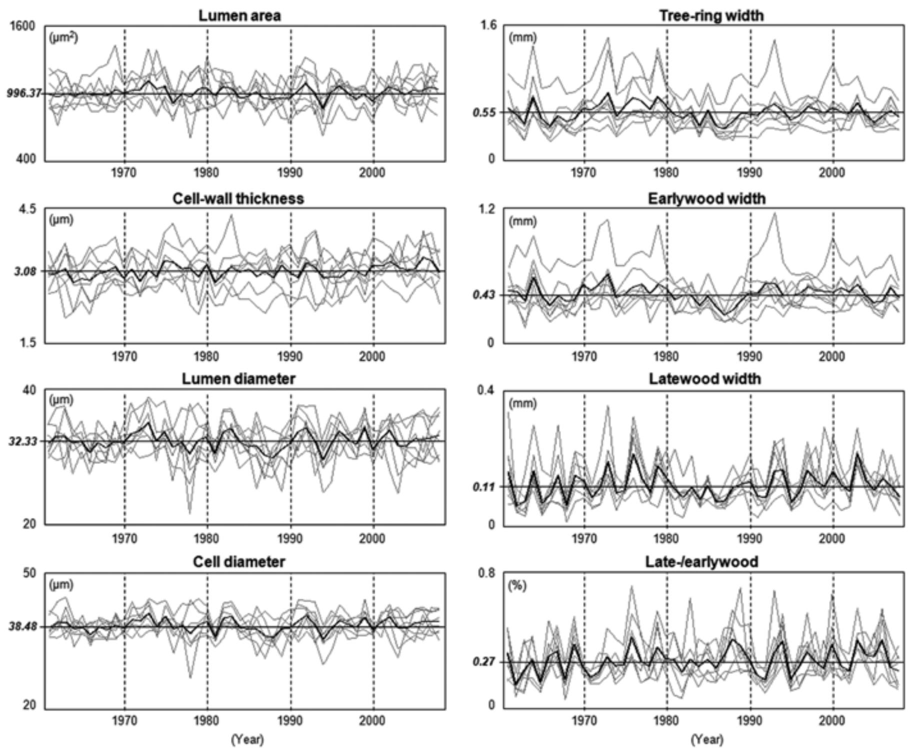

Figure 5. Raw measurements of the tree-ring and cell-anatomical variables (mean curves in bold); horizontal lines go through the respective mean values; particularly evident is the difference between both groups of variables regarding the similarity between trees per variable, expressed by R_{bt} (see Table 1).

chronologies with the measurements taken in the first 50% of tangential rows of tracheids in a tree ring.

Association between the eight chronologies

Three tree-ring variables (TR, LW, LE) and three cellular anatomy variables (LD, CD, LA) were highly positively correlated within each of these two groups (Table 3) whereas earlywood width (EW) correlated with all the variables in both groups. The subsequent factor analysis reduced the variables from eight to three (Factor 1 included CD, LD, LA [and EW], Factor 2 included LW, LE, TR [and EW], and Factor 3 included CW) (Fig. 6). The variables in Factor 1 were highly positively correlated amongst themselves; the same applied to the variables in Factor 2. However, Factors 1 and 2 were not associated with each other, except through EW. Factor 3 correlated neither with Factor 1 nor Factor 2.

Responses of tree-ring and cellular anatomy chronologies to climate

From each of the three Factors, the variable with the highest factor loading was selected and correlated with climate (Fig. 7). The response of latewood width (LW)

Table 2. Statistical qualifiers of the tree-ring and cell-anatomical variables.

TR: tree-ring index; EW: earlywood index; LW: latewood width; LE: late-/earlywood width; LA: lumen area; LD: lumen diameter; CD: cell diameter; CW: cell-wall thickness.

	Options*	MS	R_{bt}	1st (%)	SNR	EPS	R_{auto}
TR		0.19	0.43	52	5.3	0.90	0.26
EW		0.17	0.36	46	3.9	0.82	0.34
LW		0.38	0.45	52	6.5	0.87	-0.09
LE		0.34	0.39	47	5.1	0.84	-0.06
LD	10	0.05	0.11	25	1.0	0.49	0.03
	30	0.04	0.16	27	1.5	0.61	0.04
	50	0.04	0.18	29	1.8	0.64	0.20
	EW	0.04	0.17	29	1.7	0.63	0.06
CD	10	0.05	0.12	25	1.1	0.53	0.05
	30	0.04	0.18	29	1.8	0.64	0.05
	50	0.04	0.23	33	2.4	0.71	0.13
	EW	0.04	0.20	31	2.0	0.66	0.09
LA	10	0.06	0.02	20	0.2	0.15	-0.09
	30	0.05	0.07	21	0.6	0.36	0.09
	50	0.05	0.08	24	0.6	0.40	0.14
	EW	0.05	0.04	21	0.4	0.27	0.07
CW	10	0.06	0.13	24	1.2	0.55	0.25
	30	0.05	0.15	27	1.4	0.59	0.23
	50	0.05	0.14	26	1.3	0.57	0.13
	EW	0.05	0.18	31	1.8	0.64	0.13

MS: mean sensitivity, R_{bt}: corr. between trees; R_{auto}: 1st order autocorr.; 1st (%): variation in % explained by the 1st eigenvector; SNR: signal-to-noise ratio; EPS: expressed population signal; *: % of total number of tangential rows of tracheids; grey background highlights the values of the 50% option.

Table 3. Correlation between chronologies of TR (tree-ring index), EW (earlywood index), LW (latewood width), LE (late-/earlywood width), LA (lumen area), LD (lumen diameter), CD (cell diameter) and CW (cell-wall thickness).

	LD	CD	LA	EW	LW	LE	TR	CW
LD	1	**0.98** <0.001	**0.78** <0.001	**0.46** 0.001	−0.11 0.479	**−0.46** 0.001	0.14 0.356	0.23 0.124
CD		1	**0.78** <0.001	**0.47** 0.001	−0.06 0.704	**−0.39** 0.007	0.21 0.149	**0.41** 0.004
LA			1	**0.35** 0.017	−0.11 0.463	**−0.35** 0.017	0.11 0.465	0.19 0.197
EW				1	**0.55** <0.001	0.011 0.941	**0.74** <0.001	0.16 0.286
LW					1	**0.78** <0.001	**0.68** <0.001	0.21 0.162
LE						1	**0.041** 0.004	0.22 0.146
TR							1	0.35 0.015
CW								1

Bold values indicate more than 95% of confidence; dark and light shadowed backgrounds reflect the results of the factor analysis (see Fig. 6).

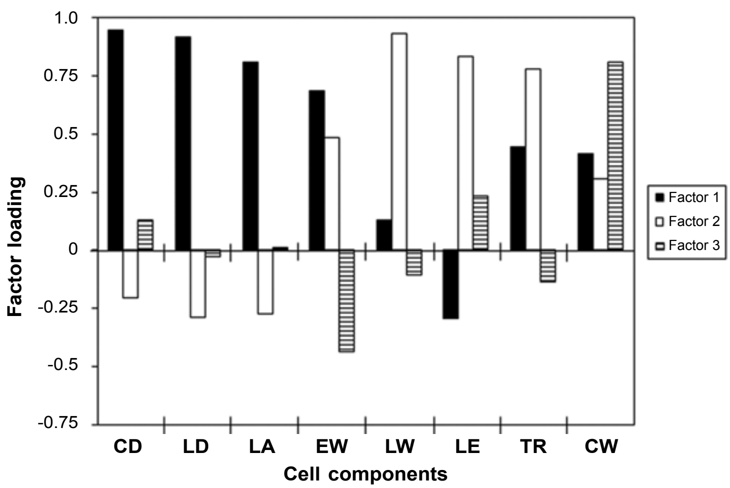

Figure 6. Factor analysis with eight tree-ring and cell-anatomical variables reducing their number to three so-called unobserved variables (or factors). Factor loading specifies the correlation between each chronology and the respective factor; CD: cell diameter; LD: lumen diameter; LA: lumen area; EW: earlywood width; LW: latewood width; LE: ratio between late- and earlywood; TR: tree-ring width; CW: cell-wall thickness.

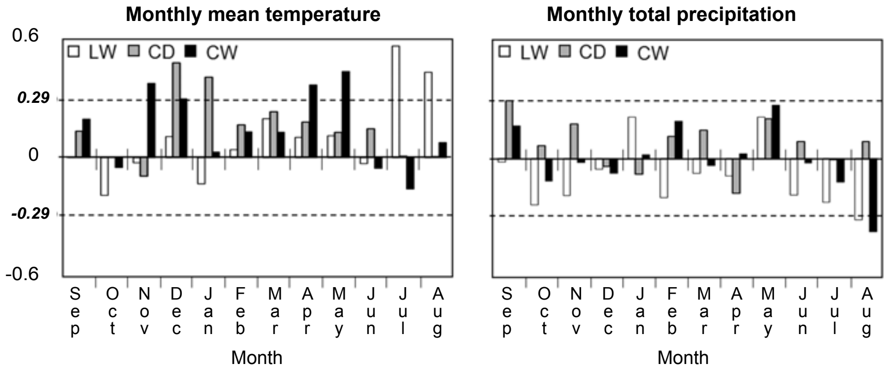

Figure 7. Correlation of tree-ring (LW) and cell-anatomical (CD, CW) variables, having the highest loading in one factor, each, and monthly mean temperature and total precipitation from 1962 to 2008; correlation coefficients beyond the dashed horizontal lines (± 0.29) are significant at the 95% level; LW: latewood width (Factor 1); CD: cell diameter (Factor 2) and CW: cell-wall thickness (Factor 3).

(Factor 2) to temperature was most conspicuous in July and August, whereas there was no response from April to June. Moreover, LW width was negatively correlated with August precipitation.

Cell diameter (CD) (Factor 1) responded significantly positively to the previous December–January temperature, but not at all to precipitation.

Cell-wall thickness (CW) (Factor 3) correlated positively to temperature both in the previous winter (November–December) and spring (April–May). The statistical association with precipitation in August is considered an artefact, because the first 50% of the tree ring has already been completely formed by the beginning of July (Seo *et al.* 2010).

On the basis of these findings, latewood width (LW), cell diameter (CD), and cell-wall thickness (CW) were selected as the most promising climatic proxies, independent from one another and reflecting different climatic signals. Whereas LW is associated with July/August temperatures (r = 0.63), CD reflected temperatures in December/January prior to growth (0.54), and CW correlated, even if only weakly, with April/May temperatures (0.48) (Fig. 8); if the year-to-year agreement is measured using the 'coefficient of coincidence' (Eckstein & Bauch 1969), the respective values are 83, 65, and 65%, clearly showing the relevance of latewood width, but also the added value provided by cellular anatomy variables.

DISCUSSION AND CONCLUSION

In our concluding considerations, we restrict ourselves to the explorative character of this study, that is to say, we focus on the statistical nature of the results and check their plausibility and consistency, without an in-depth attempt at biological explanations.

There is a large discrepancy between the values of the statistical descriptors of the tree-ring related variables and of the variables in cellular anatomy. But we know from a

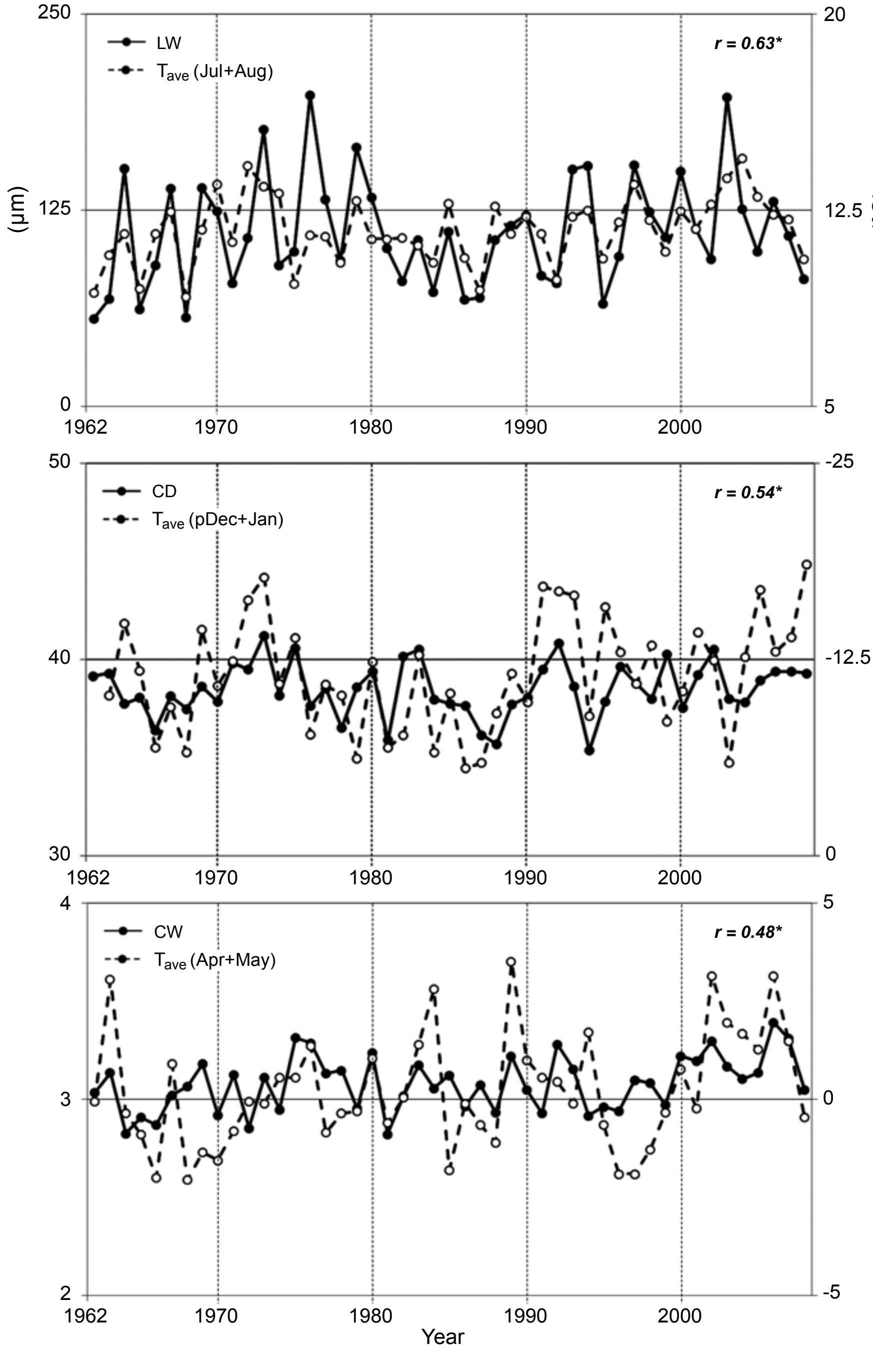

Figure 8. Latewood (LW), cell-diameter (CD) and cell-wall thickness (CW) chronologies, representing one factor, each (see Fig. 6 / Table 3) *vs*. significant temperature variables according to the climate/growth relationships (see Fig. 7).

similar study on oak (Fonti & García-González 2008) that a higher statistical quality in the tree-ring width chronology does not necessarily guarantee a stronger climatic signal, compared to the chronology of the earlywood-vessel areas of the same trees with poorer statistical quality. The high statistical quality of the tree-ring variables (see Table 2) is in accordance with results in Fennoscandian pine (*e.g.*, Kirchhefer 2001; Linderholm & Linderholm 2004), and the low statistical quality of the cell-anatomical variables complies with results for the earlywood-vessel area of chestnut (García-González & Fonti 2006). From the statistical descriptors, it is not surprising that the tree-ring related variables contain a strong summer-temperature signal (see Fig. 7a) (*e.g.* Tuovinen *et al.* 2008; Helama *et al.* 2009). However, the variables of cellular anatomy, measured in the first half of the tree rings formed from the beginning of June to early July (Stelljes 2010), reflected a strong positive correlation with temperatures during the previous December and January, *i.e.* during winter dormancy of the trees. This would mean that the climatic signal of the cell-anatomical variables is totally different from the climatic signal of the tree-ring variables, and thus provides an added value to tree-ring research. Fonti and García-González (2004, 2008) also emphasize that the different nature of environmental signals in cellular anatomy variables makes such variables worthy of consideration in addition to tree-ring width variables.

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