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RESEARCH ARTICLE

Relationship between wood anatomy, tree-ring widths and wood density of *Pinus sylvestris* L. and climate at high latitudes in northern Sweden

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ABSTRACT

In this study, wood anatomy, tree-ring width and wood density of *Pinus sylvestris* at the northern timberline in Fennoscandia were used to identify relationships among the parameters and to screen them for their climatic signals. Furthermore we investigated the influence of the juvenile wood section for all parameters developed. The measurements of wood anatomy were conducted with confocal laser scanning microscopy (CLSM) while the density profiles were produced using an Itrax MultiScanner. We developed chronologies of ring width, wood density and anatomy for a period between 1940 and 2010. Correlations between wood density and wood anatomy were strong in the latewood part. For some wood anatomy and density chronologies youth trends were found in the juvenile part. Wood density decreased from the pith up to the 9th ring and stabilized afterwards, while cell lumen diameter and lumen area increased simultaneously up to the 15th ring. All chronologies contained strong summer temperature signals. The wood anatomical variables provided additional information about seasonal precipitation which could not be found in wood density and tree-ring widths. Our study confirmed previous results stating that the parameter maximum density contains the strongest climate signal, that is, summer temperatures at the northern timberline. Nevertheless, the intra-annual data on tracheid dimensions showed good potential to supply seasonal climatic information and improve our understanding of climatic effects on tree growth and wood formation.

Introduction

Northern Fennoscandia constitutes an exceptional area for dendroclimatological studies. The strong growth correlation of trees with climate, particularly with temperature (Schweingruber et al., 1988; Briffa, 1994; Lindholm and Eronen, 2000) results from their growth at the ecological limits (Hughes, 2002). The most frequently used tree-ring parameters from the boreal climate zone are tree-ring width (TRW) and maximum latewood density (MXD). They are also used for the majority of climate reconstructions (Hughes, 2002). Several studies confirm that MXD reflect the conditions over most of the growing season whereas TRW is primarily sensitive to July temperature (Jacoby and D'Arrigo, 1995; McCarroll et al., 2003; Grudd, 2008).

Since wood is made of many individual cells, the characteristics of the wood cells, i.e., cell wall thickness and lumen area, are related to tree-ring parameters such as TRW and MXD, which result from the amount and the proportion of woody cells formed during the growing season (Deslauriers and Morin, 2005; Seo et al., 2011). By analyzing variations in wood anatomical structures, a higher intra annual resolution can be achieved than by just analyzing tree-ring width (Wang et al., 2002). In previous studies, it was shown that the dimensions of the individual tracheids were related to climate during their formation (Panyushkina et al., 2003; Eilmann et al., 2006). Studies on wood anatomical parameters from the boreal climate zone demonstrated a high potential of complementary climatic signals in cell structure measurements (Wang et al., 2002; Seo et al., 2012; Fonti et al., 2013). Such series then have the large potential to be used for reconstructions as well, if the data series were long enough, as comprehensively described for the longest wood anatomical record available so far (Panyushkina et al., 2003).

In addition to the environment, tree growth is also influenced by intrinsic factors. Several studies have examined the relationship

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between age of the individual trees and wood formation. The xylem production and differentiation in young (50–80 years) and old (200–350 years) trees of three conifer species (*Larix deciduas*, *Pinus cembra* and *Pinus abies*) from the alpine timberline were compared by Rossi et al. (2008) and it was shown that xylogenesis in old trees lasted for a shorter period and happened with lower rates of cell production. The findings demonstrated how tree-ring formation in timberline regions is related to the age of the trees, which needs to be considered when studying climate-growth relationships (Rathgeber et al., 2011). This finding was supported by Szeicz and MacDonald (1994) and Linderholm and Linderholm (2004), who also observed age dependent differences in climate sensitivity for spruce from Canada and pine from Sweden. However, so far samples of *Pinus sylvestris* growing at one site in Fennoscandia have not been examined simultaneously for TRW, wood density and wood anatomical parameters. Therefore, the objectives of this study were to establish various chronologies of wood anatomical features, wood density and TRW in Scots pine (*Pinus sylvestris* L.), for the first time, in northern Sweden and to screen them for their correlations with climate. Moreover, the influence of juvenile wood on various tree-ring parameters and the link between ring width, wood anatomy and density was investigated.

Materials and methods

Study site and plant material

The study area was located at lake Torneträsk (N 68°13′, E 19°46′, 350–450 m a.s.l.), which is north of the Arctic Circle in the upper north of Sweden. Here, trees grow on a soil influenced by discontinuous permafrost (Johansson et al., 2011), consisting of a mixture of till and fluvial deposits (Goodfellow et al., 2008). The climate belongs to the continental subarctic climate zone and is strongly influenced by the water body of Lake Torneträsk, by the short distance to the Atlantic Ocean and by surrounding mountains up to 1500 m a.s.l. (Grudd et al., 2002). The records from the nearby climate station of Abisko (Abisko Research Station, 1913–2010) located 45 km West of the study site at 385 m a.s.l. indicates an annual mean temperature of −0.5 °C., The mean July (+11 °C) as well as the mean winter temperatures (−11.9 °C) are higher than other subarctic regions at similar latitude. Additionally, due to rain-shadow caused by the orography, annual precipitation (300 mm) is quite low, having its maximum in July (Andersson et al., 1996).

The timberline is located at around 700 m a.s.l. and consists mainly of birch trees (*Betula pubescens* ssp. *tortuosa*). In general, the maximum altitude at which living pine trees (*Pinus sylvestris*) can be found is 440 m a.s.l. Since the beginning of the 20th century, many young trees have established near the upper tree-line (Grudd et al., 2002). The expansion of the growing season since 1900 seems to be the main reason for the intensive growth of young trees (Holmgren and Tjus, 1996; Callaghan et al., 2010). In the Torneträsk area 13 trees of *Pinus sylvestris* (8 trees younger than 70 years, and 5 trees older than 150 years) were sampled in autumn 2011. A 10 mm diameter increment borer was used to take two cores per tree at breast height.

Preparation of the samples and measurements

First, all increment cores (Table 1) were used to measure the tree-ring widths with the measurement system type ANIOL and the TSAP^{TM} (Time Series Analysis and Prediction – Rinn, 2007) program. The tree-ring widths of all cores were visually cross-dated and statistically verified by the program COFECHA (Holmes, 1983). Density data of six trees (Table 1) were analyzed using the Itrax MultiScanner. The preparation was performed according to the protocol of Schweingruber (1983). The cores were cut in axial direction, transverse to the direction of the fibers with a uniform thickness of 1.25 mm using a twin blade (Dendrocut2003). The resulting laths were incubated for 20 h in a Soxhlet extraction with 99.5% ethanol in order to remove all organic extractives. Subsequently, the samples were scanned in 20 μm steps by a focused X-ray beam using an exposure time of 75 ms and an intensity of 30 kV & 50 mA. As output format (X-ray negative), 16 bit digital images were obtained which were analyzed by using the commercial software WinDENDRO^{TM} to produce series of average (RGD), maximum (MXD) and minimum density (MND).

The cell anatomical measurements were performed on a subsample of nine trees (Table 1). The subsample consists of four trees from the young age class and five trees from the old age class. Tracheid anatomy and the number of cells were measured by confocal laser scanning microscopy (CLSM) along the common period from 1940 to 2010. The preparation of the samples was done according to the protocol of Liang et al. (2013a). The surfaces were cut rectangular to the growth direction of the wood fibers using the WSL core-microtome (Gärtner and Nievergelt, 2010). Afterwards, a strongly diluted safranin solution was applied to the surface to raise the contrast between cell wall and lumen. The wavelength of the helium neon laser (543 nm), of the Olympus FluoView FV300 microscope, activates the autofluorescence of wood. The CLSM captures the fluorescent images directly from the wood surface with a 100× magnification. Consecutive images were merged together using Adobe Photoshop^{TM}. Shading effects were removed by the use of an $N \times N$ average filter in CellB^{TM}. This avoids any alterations to unshaded image areas (Moëll and Donaldson, 2007). The resulting images were analyzed ring by ring within WinCELL^{TM}. For each ring, tracheid dimensions were measured along five radial files.

Table 1
List of tree samples; trees used for each parameter class were marked with "x"; tree-ring widths and wood density measured over the whole core sample (first and last visible tree rings); wood anatomical parameters measured only for the period 1940–2010.

Sample	First year	Last year	Number of rings	Average tree-ring width (mm)	TRW	Wood density	Wood anatomy
251	1970	2010	41	1.73	x		
252	1946	2010	65	1.81	x	x	x
253	1945	2010	66	1.47	x		
254	1941	2010	70	1.84	x	x	x
255	1946	2010	65	1.22	x		
256	1826	2010	185	0.76	x		x
257	1961	2010	50	2.40	x	x	x
258	1950	2010	61	2.12	x	x	x
259	1856	2010	155	0.71	x		x
260	1809	2010	202	0.77	x		x
261	1965	2010	46	2.08	x		
262	1797	2010	214	1.18	x	x	x
263	1657	1995	339	0.78	x	x	x

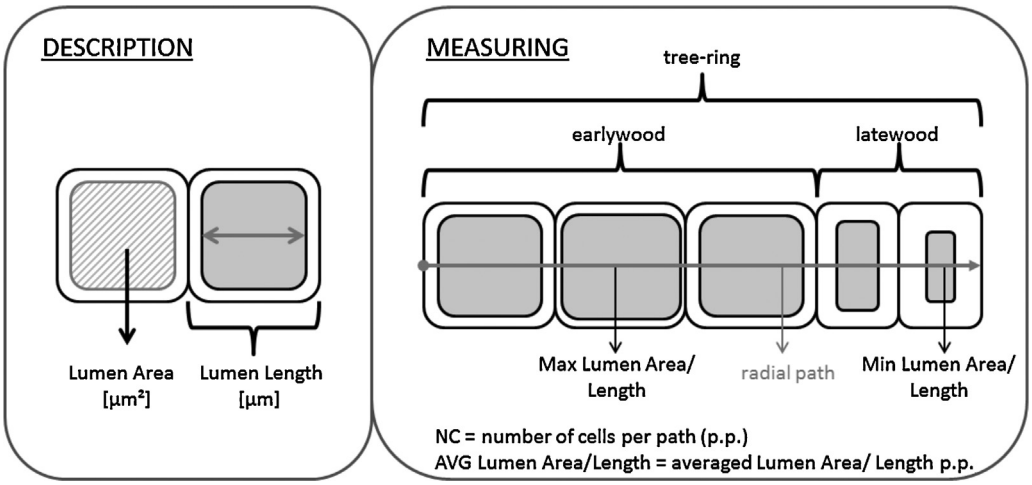

Fig. 1. Description: schematic figure of the *parameter measured by WinCell*. Measuring: schematic figure of the tree ring and the different locations of the parameter.

Earlier studies of *Pinus sylvestris* showed that 5–6 paths (Fig. 1) are enough to be statistically reliable (Vaganov et al., 2005). For narrow rings with less than 10 cells per path, the number of paths was increased (max. 13 paths) to enhance the statistical significance. For each year the number of cells (NC) for all paths were counted and averaged into a yearly value. The lumen length and the lumen area were measured for all tracheids. For each path average (AVG), maximum (Max) and minimum (Min) values of the tracheid parameters were produced (Fig. 1 and Table 2). The yearly values of the tracheid parameters were averaged from all paths of the year.

Standardization and chronology building

The detrending was done according to the specific demands of the chronologies (Table 2). Following Cook and Peters (1997), power transformation was used to stabilize the heteroscedastic variances of the raw tree-ring series. Moreover, age-related trends (were present) were removed by the Hugershoff function in ARSTAN (Bräcker, 1981; Cook et al., 1990). Series with no age trend were indexed by their means.

Each of the ten chronologies was characterized by the standard deviation (stdev), the mean sensitivity (ms), the first-order autocorrelation [ac (1)] and the inter-series correlation (r). Except ac (1) and stdev, all statistical parameters should be high to predict a strong dendroclimatological potential (Grissino-Mayer, 2001). According to these statistics, trees were either included in the resulting cell chronology or rejected. Following the recommendations of Drew et al. (2013), only trees correlating $r \geq 0.1$ with the master chronology were used for further analyses.

Climate-growth relationship

Daily temperature and precipitation data of the Scientific Research Station in Abisko for the period 1913–2010 were obtained from the Swedish Polar Research Secretariat. The climate responses of TRW, wood density and wood anatomical chronologies were examined using the program CLIMTREG for the common period of 1940 and 2010 (Beck et al., 2013). CLIMTREG uses daily climate data to calculate short (minimum 21 days) and long (maximum 121 days)-term climate-growth correlations. After calculating the standard amount of correlations (42,218 individual correlations) for each climate parameter CLIMTREG demonstrates the time spans with the highest correlations between the tree-ring parameters and the climate parameters.

Results

Chronologies

The mean tree-ring width of the trees studied was 1.45 ± 0.05 mm and built from 36 ± 0.24 cells, based on a total of 115,631 cell measurements from 3135 cell rows (Table 3). The AVG Lumen Length was 17.91 µm and the AVG Lumen Area 295.62 µm^2 [591.13 ± 0.12 µm^2 earlywood (Max Lumen Area) and 54.92 ± 0.17 µm^2 latewood lumen area (Min Lumen Area)]. The

Table 2
Preparation of various tree-ring variables – TRW (tree-ring widths), MXD (maximum density), MND (minimum density), RGD (ring density), NC (number of cells).

Parameter class	Parameter	Trend	Heteroscedastic variances	Preparation
Tree-ring width	TRW	Age trend	Yes	1. Power transformation 2. Detrending by Hugershoff function
Wood density	MND RGD	Youth trend	No	1. Detrending by Hugershoff function
	MXD	No trend	Yes	1. Power transformation 2. Indexation by mean
Wood anatomy	AVG lumen area Max lumen area AVG lumen length Max lumen length	Trend	Yes	1. Power transformation 2. Detrending by Hugershoff function
	Min lumen area	No trend	No	2. Indexation by mean
	NC	Age trend	Yes	1. Power transformation 2. detrending by Hugershoff function

Table 3
Chronology statistics of the standardized tree-ring parameter, number of trees (no. of trees), raw mean cell parameter (mean), standard deviation (stdev), mean sensitivity (ms), first order autocorrelation (ac (1)), Gleichläufigkeit (Glk), Cross Date Index (CDI) and intercorrelation (*r*).

Parameter class	Parameter	No. of trees	Mean (raw)	Min (raw)	Max (raw)	Stdev	MS	Ac (1)	Glk	CDI	*r*
Tree-ring width (mm)	TRW	13	1.45	0.55	3.30	0.26	0.17	0.66	75.00	76.00	0.46
Wood density (g/cm^3)	RGD	6	0.46	0.35	0.60	0.08	0.07	0.22	80.00	76.00	0.46
	MND	6	0.27	0.23	0.36	0.10	0.08	0.23	73.00	47.00	0.48
	MXD	6	0.66	0.46	0.89	0.13	0.12	0.13	81.00	79.00	0.49
Wood anatomy ($\mu m^2/\mu m$)	AVG lumen area	6	295.62	187.05	399.33	0.12	0.11	0.38	66.00	35.00	0.33
	Max lumen area	6	591.13	394.98	793.24	0.12	0.11	0.33	68.00	42.00	0.34
	Min lumen area	6	54.92	37.23	85.99	0.17	0.17	0.00	71.00	40.00	0.28
	AVG lumen length	8	17.91	13.02	21.64	0.08	0.07	0.41	71.00	45.00	0.45
	Max lumen length	6	29.72	21.28	35.96	0.08	0.07	0.48	66.00	38.00	0.37
	NC	6	35.74	17.67	63.81	0.24	0.17	0.62	72.00	45.00	0.46

mean ring density (RGD) from six trees was 0.46 ± 0.08 g/cm^3. The maximum wood density was found in the latewood and was 2.4 times higher (MXD = 0.66 ± 0.13 g/cm^3) than the minimum density, which was found in the earlywood (MND = 0.27 ± 0.10 g/cm^3).

The intercorrelation of the series was similar among the tree-ring parameters, slightly higher for TRW and wood density than for the wood anatomical chronologies. The lowest mean sensitivities were indicated for the AVG and Max Lumen Length as well as for MND and RGD. The results for the first-order autocorrelations suggest large differences among the tree-ring parameters. While TRW and NC exhibited high autocorrelations, Min Lumen Area, RGD and MND had low autocorrelations and consequently are potential useful for climate reconstructions due to a higher information content for the year of the ring formation (Conkey, 1979; Grissino-Mayer, 2001).

Correlations between the chronologies

The wood anatomical parameters displayed positive correlations with TRW and between each other (except for Min Lumen Area), whereas the correlation with density was mostly negative (Table 4). TRW was significantly and positively correlated with AVG and Max Lumen Length and NC, whereas no significant correlation with any density chronologies was revealed. The density chronologies (MXD and RGD) demonstrated significant negative correlations only with Min Lumen Area. MND of the earlywood section and MXD of the latewood section were significantly and positively correlated with RGD, representing the density of the whole ring.

Youth trends

Youth trends could only be examined for those trees, where the juvenile wood, close to the pith, was visible. All four trees of the young age class fulfilled these criteria. In addition, one old tree, which served as a reference (Panyushkina et al., 2003), was analyzed over all 214 years to evaluate if the youth trend was independent from time. The wood density and wood anatomy data were screened for youth trends. Within the latewood section no youth trend was revealed in wood density and wood anatomy data, and thus was not studied further. We focused on trends in the raw earlywood density and wood anatomical data of only the four young trees. The analyses were based on cambial age dating, where the cambial age represents the ring number starting from the pith (Spicer and Gartner, 2001).

Following the recommendations of Yang et al. (1986) the intersection of two regression lines was defined as a boundary point between the juvenile wood with its inherent youth trend and the mature part of the tree. For the wood anatomical parameter (Max Lumen Area/Length) the intersection point between both trends suggested a cambial age of 15 (Fig. 2A), thus, the youth trend has a length of 15 years. It was characterized by a strong increase in Max Lumen Length as well as in the Max Lumen Area whereas the mature part indicated a stabilization (Max Lumen Length) or a flattened increase in Max Lumen Area.

In contrast to the wood anatomical data the youth trend in density was defined by a decrease in MND which showed a youth trend within the first 9 years (Fig. 2B). When comparing the youth trends in MND and the wood anatomical features Max Lumen Area and Length, temporal changes in the relationships are displayed (first 9 years indicated by dots of lighter color in Fig. 2C). Within the first 9 years the changes are most significant. The youth trend for Max Lumen Length was smaller than for Max Lumen Area while MND was decreasing from 0.40 to 0.28 g/cm^3. The changes in MND due to the youth trend were strongest for the first 9 years. Afterwards fewer changes in wood density were indicated while lumen lengths continued to increase significantly until a cambial age of 15. Within the mature section the relationship between MND and Max Lumen Length was characterized by a low variability in the lumen size and a stronger variability in density (indicated by dots of darker color in Fig. 2C). It was found to be the opposite for the relationship between mature Max Lumen Area and MND, that is, MND was stable and the Max Lumen Area displayed fluctuations. Since the Max Lumen Area integrates the measurements of radial and tangential cell lumen measurements, the comparison of the two relationships with MND indicates that only measuring radial lumen for the parameter Max Lumen Length results in different results which might be due to the additional integration of tangential lumen or cell wall measurements.

Climate response

Daily climate correlations were performed with the standardized ring variables (Table 5). It should be noted that CLIMTREG only shows the five highest correlations between the ring variables and climate variables and that we only included the strongest correlations here. Further lower and probably also significant correlations were not shown. The Min Lumen Area and MND show significant negative correlations to summer temperature and precipitation. The correlation between RGD and previous autumn and winter precipitation, were also negative. The climate responses of all other parameters to temperature and precipitation were positive.

Except for Max Lumen Area, all chronologies showed strong responses to summer temperature. The strongest connection to summer temperature was represented by MND ($r = -0.551$) and MXD ($r = 0.667$) and covered a period from May to September. The strongest correlations toward precipitation were found in the wood anatomical variables AVG Lumen Area ($r = 0.501$) for the current year precipitation from July to September, and Max Lumen Length ($r = 0.508$) for previous July-to-October precipitation.

Table 4
Pearson's correlation coefficients for the standardized wood anatomy, density and tree-ring width chronologies; significant coefficients (95%) appear in bold.

Parameter	AVG lumen area	AVG lumen length	Max lumen area	Min lumen area	Max lumen length	NC	TRW	MXD	MND
AVG lumen length	**0.696**								
Max lumen area	**0.799**	**0.615**							
Min lumen area	0.237	0.117	0.258						
Max lumen length	**0.607**	**0.740**	**0.662**	0.036					
NC	0.181	**0.441**	0.225	−0.107	**0.563**				
TRW	0.121	**0.383**	0.179	0.000	**0.414**	**0.786**			
MXD	−0.129	−0.070	−0.011	**−0.494**	0.171	0.290	0.208		
MND	−0.069	−0.102	−0.194	0.085	−0.141	−0.087	−0.065	−0.060	
RGD	−0.275	−0.253	−0.197	**−0.304**	−0.056	0.196	0.124	**0.609**	**0.586**

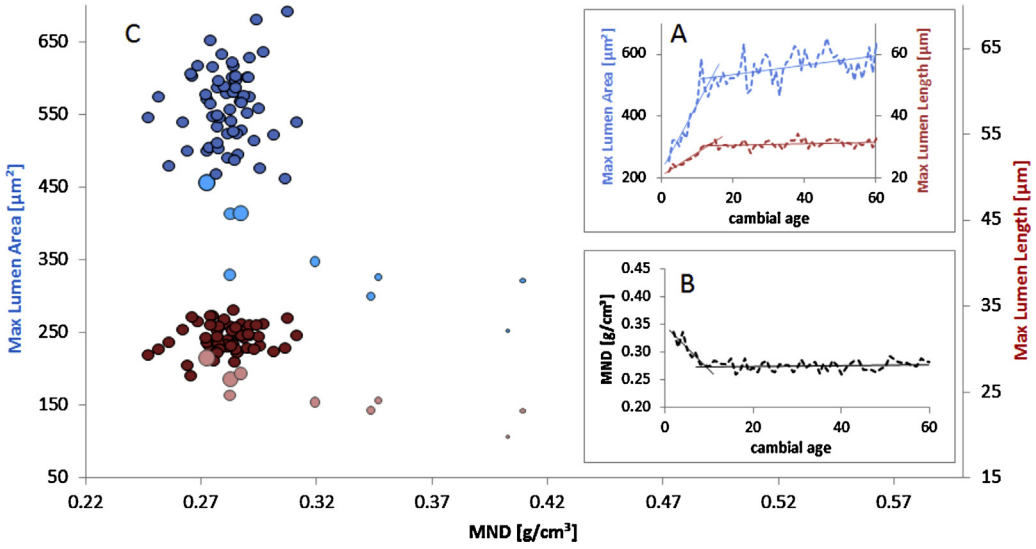

Fig. 2. (A) Linear regressions for the raw Max Lumen Area (blue line) & Max Lumen Length (red line) chronologies; (B) linear regressions for the raw MND (gray line); (C) youth trends in wood features in relation to youth trends in MND; Max Lumen Area (blue dots); Max Lumen Length (red dots); light spots of each color representing the youth part and the size of the dots increase with increasing age. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 5
Correlation between tree-ring variables and climate parameters for period 1940–2010; bold values indicate four most significant correlations (critical signal values: 95%: 0.237, 99%: 0.308). Months in capital letters indicate current year, small letters indicate previous year.

Parameter	Station data Abisko (1940–2010)		Time span (days)	
	Temperature	Precipitation	Temperature	Precipitation
Min lumen area	02 JUNE to 27 AUGUST −0.447	13 AUGUST to 08 SEPTEMBER −0.367	87	27
Max lumen area	–	19 august to 06 october 0.460	0	49
AVG lumen area	01 july to 19 october 0.312	07 JULY to 25 SEPTEMBER **0.501**	111	81
AVG lumen length	24 july to 03 november 0.371	19 august to 24 september 0.469	103	49
Max lumen length	25 MAY to 12 JULY 0.306	18 july to 05 october **0.508**	49	80
NC	05 JULY to 26 AUGUST 0.394	30 august to 19 september 0.383	53	21
MND	10 JUNE to 29 JULY **−0.551**	26 october to 16 december −0.371	50	52
MXD	30 MAY to 05 SEPTEMBER **0.667**	10 AUGUST to 21 OCTOBER 0.341	99	73
RGD	31 JULY to 28 AUGUST 0.358	07 november to 11 december −0.353	29	35
TRW	05 JULY to 29 JULY 0.339	09 september to 05 october 0.444	24	26

Discussion

Chronologies

The successful synchronization of tree-ring width patterns formed the basis of all further analyses. Ring width data of *P. sylvestris* were gathered from previous studies conducted by Grudd et al. (2002). The density and TRW variables were characterized by high intercorrelations. The statistics for the wood anatomical chronologies showed weaker intercorrelations. This was also documented in the literature (Fonti and García-González, 2008; DeSoto et al., 2011; Bryukhanova and Fonti, 2012; Seo et al., 2012; Liang et al., 2013b). According to Martin-Benito et al. (2012) this is due to the smaller variability of tracheid size in comparison to density and TRW data, resulting in low sensitivities. However, according to previous findings (Yasue et al., 2000; Martin-Benito et al., 2012; Olano et al., 2012; Seo et al., 2012) the values of the present research were in the standard order of magnitude.

Correlations between the chronologies

Several studies have reported a larger proportion of earlywood than latewood for conifers (Kalela-Brundin, 1999; Wang et al., 2002; Park and Spiecker, 2005; Olano et al., 2012). The research of Seo et al. (2011) has shown that *P. sylvestris* growing in northern Finland, 75% of the entire ring width is earlywood. Our data confirm the previous studies. The high correlation ($r = -0.799$) between Max Lumen Area representing the earlywood section, and AVG Lumen Area, which is representative for the entire ring is likely to be explained by the higher proportion of the earlywood section within the whole ring (Table 4). The correlation between Max Lumen Length and AVG Lumen Length was found to be similarly high ($r = -0.740$).

The analysis revealed a high positive correlation between both lumen classes (area and length), that is, if the length of the lumen increased, the area of the lumen increased as well.

Although the correlation between the two parameters was high the remaining unexplained variability is most likely due to the differences regarding the tangential lumen length. This has been found in previous studies as well. The tangential direction within a ring may vary up to 15% (Moëll and Borgefors, 1999; Rathgeber et al., 2006).

The correlations between TRW and wood anatomical parameters, e.g. AVG and Max Lumen Length were much weaker than the correlation between TRW and NC. In general, the dependency of TRW toward lumen length resulted from the impact of cell formation on tree-ring width. In agreement with Panyushkina et al. (2003) and Knorr (2013) the present research reported a strong correlation between TRW and NC. According to Martin-Benito et al. (2012) this is because wider tree rings were mainly driven by a high cell division rate rather than cell enlargement.

The strongest connection between wood anatomy and wood density data is displayed by the significant negative connection between MXD and Min Lumen Area (latewood cells). When the size of tracheids in the latewood increases the proportion of the cell walls decreases because of the enlargement of lumen sizes and thus MXD is reduced systematically. This effect resulted in a significant negative connection, where the Min Lumen Area explained 24% of the variability of MXD.

The low correlation between TRW and MXD is most likely a result from the age composition of the samples used for density measurements (4 young trees and 2 old trees. The TRW were strongly influenced by the age trend during the first 30 years of tree life. In contrast, the MXD is independent from this overlying trend. The high correlation between MXD and TRW often described in other studies (e.g., Melvin et al., 2013) could only be verified in our study for the parts of the trees, where the impact of the age trend was less significant.

Youth trends

The youth trend in cell structures is responsible for the trend in the minimum density data (Krause et al., 2010). The difference between the youth trends of lumen and minimum density is probably due to the increase in wall thickness over time (Mitchell and Denne, 1997), buffering this trend. Studies of Hannrup et al. (2001), Lindström (1997) and Vysotskaya and Vaganov (1989) also showed cambial age dependences for earlywood lumen length in *P. sylvestris*.

Several hypotheses (e.g. pipe model theory (Shinozaki et al., 1964) or the West, Brown and Enquist model (WEB model – 1999)) striving to explain this trend are focusing on water transport as one of the functions of tracheids. They assume that the size of the lumen decreases upwards the tree to minimize the risk of xylem dysfunctions due to embolism. The path length of a growing tree increases and the negative pressure lifting the water up to the leaves decreases. To stop the process of a path length induced decrease of the negative water pressure, the conduits taper acropetally from the trunk base to the canopy (Anfodillo et al., 2006; Schuldt et al., 2013). The implementation of the convergent tapering of the xylem conducts is controlled by the influence of hormones (Lindström, 1997), e.g., auxin (Liang et al., 2013b). It seems that in our study this effect was worn out after approximately 15 years, most likely, because the tree has grown taller and the wood formation in breast height is no longer affected by this tapering but only higher parts of the stem are forming tracheids with smaller lumen.

Climate response

The results of the correlation analyses between daily climate data and tree-ring variables exhibited a high temporal resolution of climate-growth interactions, closely related to the time window when xylem formation of *P. sylvestris* was most likely sensitive to precipitation and temperature. Almost all tree-ring variables were significantly positively or negatively correlated within the months May to September of the current or previous year, which was also found by Schmitt et al. (2004). In contrast to the findings of Panyushkina et al. (2003) the temporal resolution of the climate-growth correlations was not higher for wood anatomical parameters than for TRW and MXD. The results suggest that wood density and TRW are determined by additional cell characteristics (e.g., wall thickness, micro fiber angle) than is the variability of the tracheid lumen.

The time window in which most tree-ring variables correlated best with precipitation was smaller than for temperature. The precipitation signal was most significantly implemented in the parameters AVG Lumen Area and Max Lumen Length. The influence of the precipitation is mediated through the osmotic potential which is the key mechanism controlling the turgor pressure within the cells. High amounts of precipitation result in a stronger cell enlargement causing a higher turgor pressure (Hölttä et al., 2010).

The correlation between Min Lumen Area and MXD indicates a dependency between wood anatomical characteristics and wood density. Both parameters reveal a dependency toward summer temperatures of the growing season. While the cell enlargement is usually finished within a few weeks, the following period of secondary cell wall thickening will last longer (Vaganov et al., 2005). The length of this period depends on the duration of temperature conditions favoring growth. In our study, the prolongation of

this period of secondary cell wall thickening probably resulted in decreasing lumen sizes of the latewood cells, which was represented by a negative correlation between MXD and Min Lumen Area as well as the negative correlation toward summer temperatures.

Minimum density, which occurs in the earlywood, has been formed during June and the beginning of July (Schmitt et al., 2004). It shows a negative correlation with June-to-July temperatures of the current year. In this regard our results corroborate the report of Antonova and Stasova (1993).

Conclusions

In this study, cellular anatomy, tree-ring width and density were used to identify the relationships among these parameters and to screen for their climatic signals. Chronologies of wood anatomical features have been established for the Torneträsk area for the first time. The correlations between wood anatomical features and wood density were strongest for the latewood part. The highest correlation coefficient of $r = -0.494$ between Min Lumen Area and MXD indicated a significant correlation, explaining 24% of the MXD variations by changes in Min Lumen Area. The wood density parameters were correlating best with the climate conditions of the current year. In general, the correlations with temperature data were found to be stronger for wood density and TRW than for the wood anatomical features. Furthermore, it was revealed that AVG Lumen Area and Max Lumen Length contain a strong precipitation signal, which has so far not been demonstrated for the other tree-ring proxies at this site. In regard to the trend in wood anatomical features and minimum density, the earlywood tracheids could be verified as the cause for the youth trends. In future studies, the presence of juvenile wood needs to be accounted for, when using minimum density or earlywood anatomical parameters as climate proxies.

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