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A COMPARISON OF TREE-RING FEATURES IN PICEA ABIES AS CORRELATED WITH CLIMATE

by

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SUMMARY

This paper presents an analysis of 16 anatomical variables measured on 20 spruce trees [*Picea abies* (L.) Karst.] from sites in the managed forest district Seyde, Eastern Ore Mountains, south of Dresden, Germany. Ring width and latewood proportion did not show significant relationships with monthly climatic data, whereas maximum density, latewood cell-wall proportion and latewood density were highly correlated with temperature and precipitation. The climatic signals expressed in resin duct density, ray height, tracheid length and microfibril angles were less pronounced. Of 16 tree-ring parameters, densitometry – as an indirect measure of xylem anatomy – has again shown its great potential to record climatic conditions.

Key words: Tree-ring analysis, dendrochronology, densitometry, wood anatomy, climate.

INTRODUCTION

The most frequently used variable in tree-ring studies is ring width (Fritts 1976), as well as the relative proportions of earlywood and latewood zones (e.g. Oleksyn & Fritts 1991). Other studies include tracheid dimensions in softwoods (Vaganov 1990) or vessel size and arrangement in hardwoods (Woodcock 1989; Woodcock & Ignas 1994; Sass & Eckstein 1995). Wood density profiles have been frequently measured in softwoods (e.g. Cleaveland 1986; Schweingruber 1989; Briffa et al. 1998a, b) and also in hardwoods (e.g. Funada et al. 1995; Guan et al. 1996). Intra-annual density fluctuations (more commonly called false rings) can be used for crossdating and age-determination (e.g. Young et al. 1993; Van der Burgt 1997) but also to indicate environmental changes (Villalba & Veblen 1996). Conifers may develop 'light rings', an anatomical feature characterised by very low maximum latewood density induced by climatic events such as volcanic eruptions (Filion et al. 1986; Delwaide et al. 1991; Evans et al. 1996; Gindl 1999). Freezing during the growing season sometimes causes distorted cells in the latewood, resulting in a 'frost ring' (LaMarche & Hirschboeck 1984; Brunstein 1996). The number of resin ducts per unit area correlates with temperature (Wimmer & Grabner 1997) and intra-annual radial cracks in coniferous trees accompanied with traumatic resin ducts may be used as an indicator for wind, drought or frost events (Cherubini et al. 1997). Most studies usually consider a narrow selection of tree-ring features, rather than being comparative studies using a large set of features. This research, however, included 16 parameters measured in dated tree-ring series of even-aged spruce trees grown on managed forest land, to determine which ones are correlated with climate.

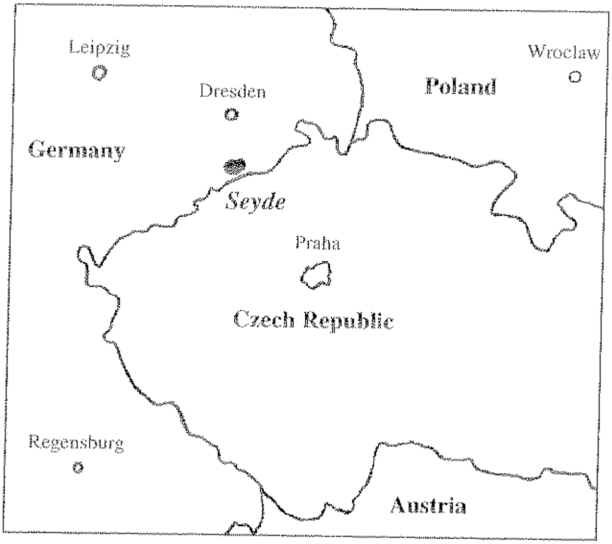


Fig. 1. Map of the site area Seyde, Germany, in the East Erzgebirge close to the Czech border.

MATERIALS AND METHODS

Trees were studied from two sites in the forest district Seyde, Eastern Ore Mountains, Saxony, 50 km south of Dresden, Germany, close to the Czech border (Fig. 1). The sites were even-aged, approximately 70 years old, with Norway spruce, *Picea abies* (L.) Karst., both located on quartzporphyric bedrock. The natural forest community is a mixed beech-fir-spruce forest at altitudes of 700–820 m. Spruce trees cover 80% of the area and the predominant brown forest soils are partially podsolised. In 1976 and later, thinning and clear-cut activities took place south-east of one site. As a consequence, site factors presumably have changed, including radiation, water regime, stronger winds, ice damage, nutritional status and deposition rates of gaseous SO_2. Therefore, data were take only for rings 1–40 to avoid growth effects of these disturbances.

The Ore Mountains are located in a transition from Atlantic to continental climate types. Annual total precipitation is 965 mm, 38% of which is snow. Annual mean temperature is 5.5 °C, with –23 °C as the lowest temperature measured (Fig. 2). Main wind directions are north and north-west with an average wind speed of 6 m/s.

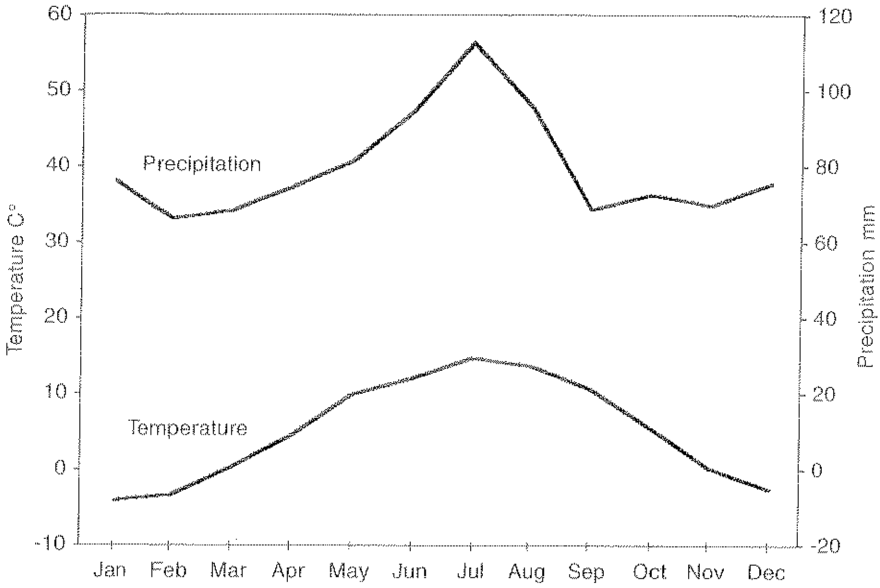


Fig. 2. Temperature-precipitation diagram of the station Seyde, East Erzgebirge, Germany, 53° 12' North, 11° 45' East, 750 m a.s.l.

In total, 20 dominant and codominant trees were felled in April 1993 and complete stem disks were removed at about 4 m above ground from each tree. Disks were immediately transported to the laboratory for sample preparation. Cross dating was carried out according to standard procedures (Stokes & Smiley 1968; Swetnam et al. 1985), securing exactly dated samples for all measured features.

Anatomical parameters were measured on transverse and longitudinal sections – 20 μm in thickness – cut from 1 × 1 cm cubes using a sledge microtome. Sections were dehydrated, stained with methylene blue and mounted in Malinol on slides (Gerlach 1984). With a series of transverse sections, all tree rings between the pith and the bark were examined. Likewise, tangential sections were prepared from each individual tree ring. Two radii (north and south) were prepared from each disk. Most anatomical parameters were measured using a light microscope with a CCD-camera connected to a Macintosh computer that was loaded with the NIH-Image analysis system (Wayne Rasband, National Institutes of Health, USA, available from http://rsb.info.nih.gov/nih-image/default.html). In the cross section, cell-wall proportion in earlywood and latewood and the number of resin ducts per mm^2 (= resin duct density, Wimmer & Grabner 1997) were measured. On longitudinal sections the mean height of uniseriate rays (Van den Oever et al. 1981), the total number of ray cells per unit area, microfibril angle (Senft & Bendtsen 1985) and tracheid length (Ladell 1959) were measured in earlywood and latewood. From adjacent disks taken from each felled tree, microdensitometry was performed according to Schweingruber (1989) and ring widths, latewood proportion, earlywood and latewood density as well as minimum and maximum density determined. The full set of 20 trees was measured for the features obtained through densitometry, cell-wall proportion and resin ducts. Wood ray features were only measured on 6 trees and microfibril angles and tracheid lengths on 10 trees. To all tree-ring raw data we fitted a negative exponential curve or a linear regression. The features were converted to indices by dividing each measured value by the fitted model value (Fritts 1976; Cook 1985). This process removed most of the long-term trends and scaled to constant variance and a mean of 1 for all features.

All parameters proved to be normally distributed (Kolmogorov-Smirnov test), allowing calculation of Pearson correlations with monthly climatic data. The variables were transformed to principal components and then used in a hierarchical cluster analysis to identify homogeneous groups among the anatomical variables. Cluster analysis is the searching for groups (clusters) in the data in such a way that objects belonging to the same cluster resemble each other, whereas objects in different clusters are dissimilar. Hierarchical algorithms proceed by combining or dividing existing groups, producing a hierarchical structure displaying the order in which groups are merged or divided.

A simple correlation analysis was employed but this analysis does not separate direct from indirect relationships. To control for effects of common cause, path analysis was used (Zhang & Zhong 1992). Path analysis is an extension to multiple regression and helps to analyse the structure of data. Through path analysis the magnitudes of the linkages between variables are estimated and these estimates are used to provide information about the underlying causal process (Miller & Jastrow 1990). The wood density features were seen as dependent and all other anatomical characteristics as independent. The resulting standardised regression weights or path coefficients indicate the strength and direction of the relationships among the hypothesised variables. The path-coefficients show the degree to which a variable hypothesised as a cause has a direct effect on a dependent density variable. These coefficients tell the amount of change expected in the density variable relative to its standard deviation, for a change in one standard deviation in the independent variable. Because they are standardised the amount of change in the dependent variable can be directly compared. For statistical calculation SPSS® (Release 8.0, 1997) and for path analysis EQS® (Multivariate Software Inc. Ver. 5.7b (C) 1985-1998; (Bentler and Wu 1995) was used.

RESULTS

Figure 3 gives an overview of all measured and indexed parameters for the 40-years period. The graphs are plotted with offsets for better visibility. Simple correlation coefficients were calculated with monthly temperature means and precipitation sums. We used 14 months starting with the preceding September to account also for carry-over effects of the previous year. Above average rainfall in July and August is related to higher latewood proportions (Fig. 4). No relationships existed between growth rate,

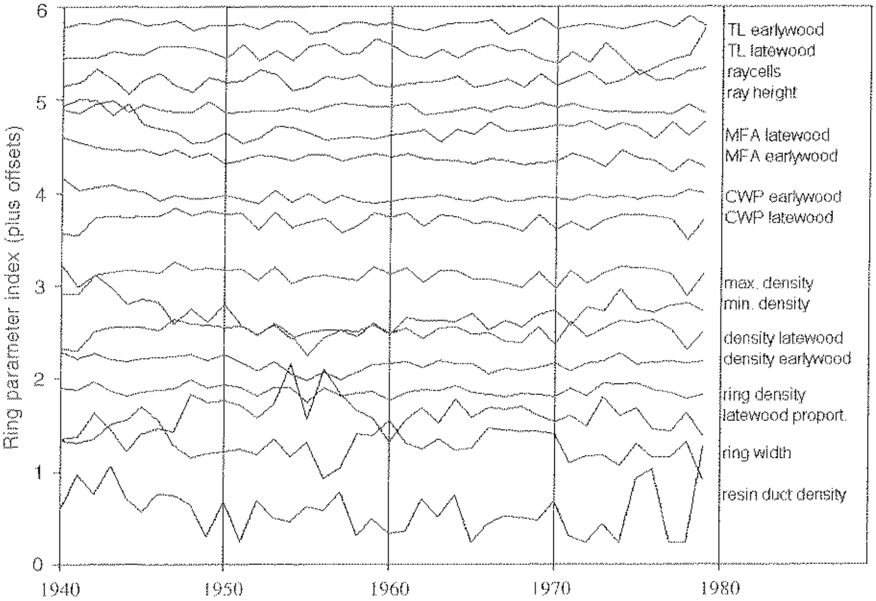


Fig. 3. Variability of the 16 measured indexed tree-ring features, 1940–1979, plotted with offsets. TL = tracheid length, MFA = microfibril angle, CWP = cell wall proportion.

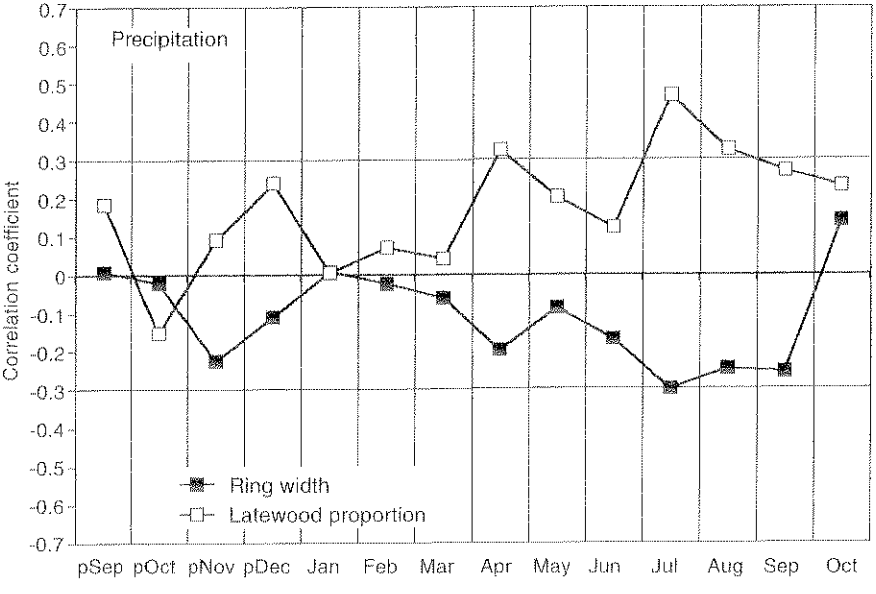
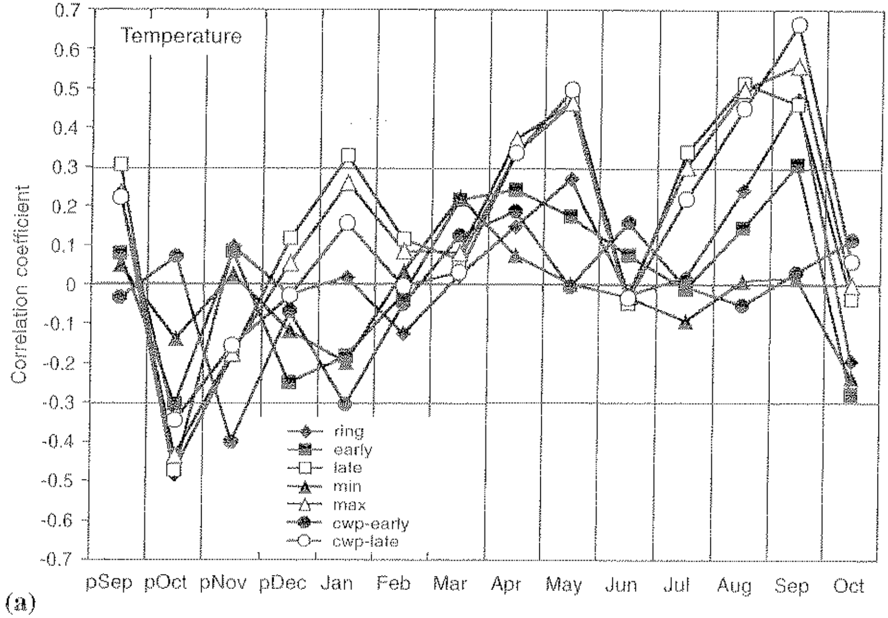


Fig. 4. Correlation function for ring width and latewood proportion with precipitation, from previous September through current year October (14 months), 1940–1979.



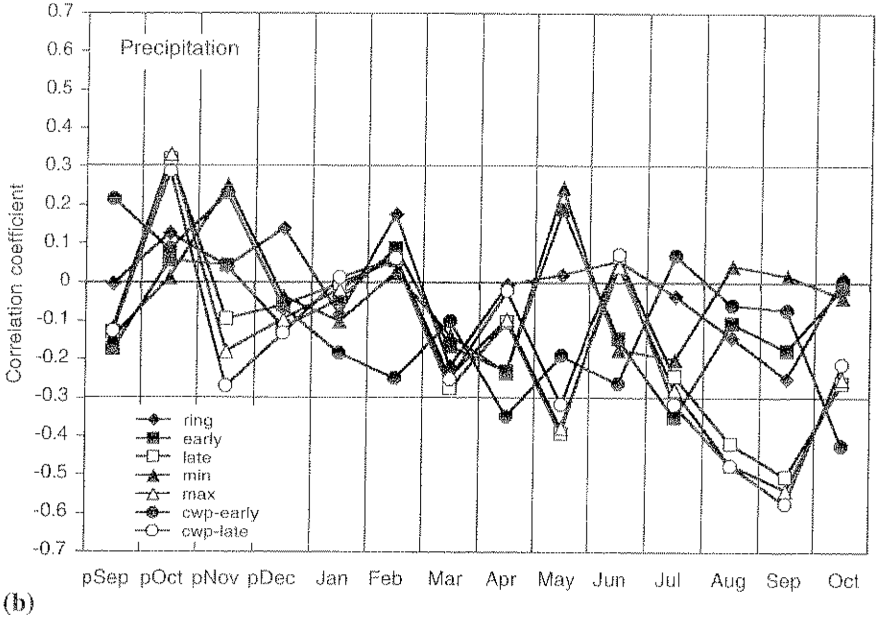
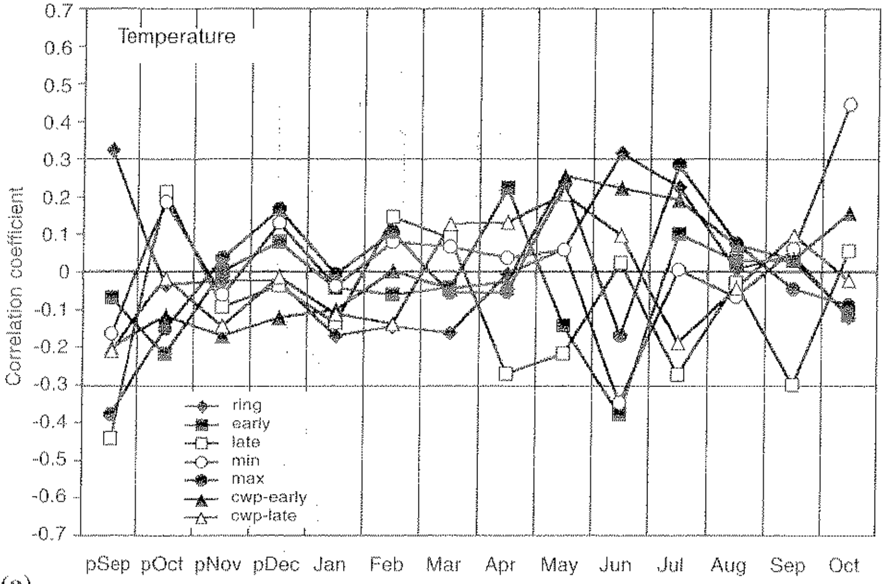
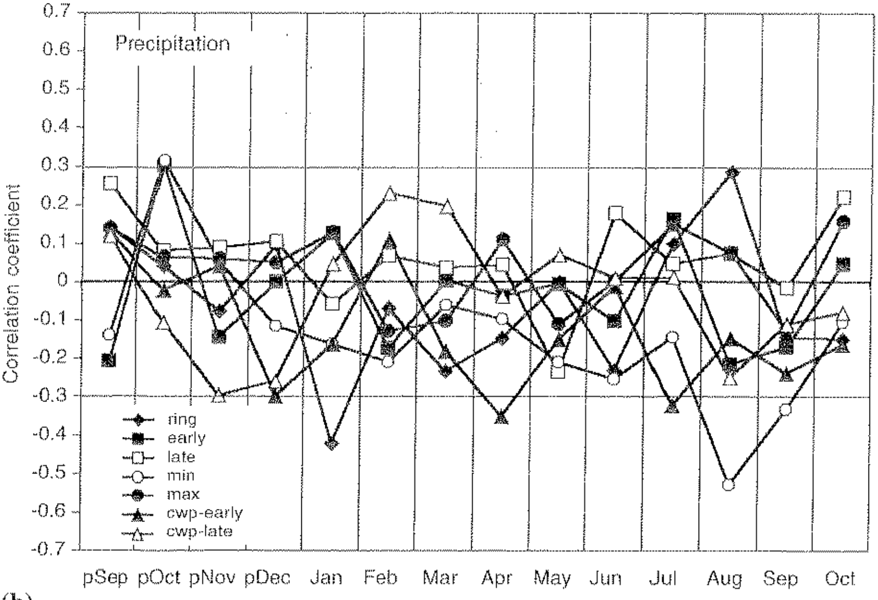


Fig. 5. Correlation function for mean ring density (mean), earlywood (early) and latewood (late) density, minimum (min) and maximum (max) density, cell wall proportion in earlywood (cwp-early) and latewood (cwp-late), from previous September through current year October (14 months), 1940–1979: (a) temperature, (b) precipitation.



(a)



(b)

Fig. 6. Correlation function for resin duct density, microfibrillar angle in earlywood (mfa-ew) and latewood (mfa-lw), average height of uniseriate rays (ray-height), number or ray cells (raycells) and tracheid length in earlywood (length-ew) and latewood (length-lw), from previous August through current year October (14 months), 1940–1979: (a) temperature, (b) precipitation.

latewood proportion and temperature. Figure 5 depicts all densitometry parameters plus cell-wall proportion measured in earlywood and latewood. Strong signals can be seen with both climate parameters. Summer temperature (Fig. 5a) has a high impact on cell-wall proportion of latewood, maximum density and average latewood density. Poor climatic response is seen with earlywood density. Minimum density and earlywood cell-wall proportion have the weakest correlation with both temperature and precipitation. August and September precipitation (Fig. 5b) are also correlated negatively with cell-wall proportion in latewood, latewood density and maximum density.

The reactions of resin duct density, microfibril angle, wood ray height and raycell number to climate were weak relative to those of the density parameters (Fig. 6a, b). Resin duct proportion is positively correlated with June temperature but not with rainfall. August and September rainfall seems to influence negatively and October temperature positively the ray height while the number of wood ray cells per unit area (raycells) is insignificant. October temperature influences the same feature in positive direction. April and July precipitation seem to have negative effects on earlywood tracheid length. In summary, the strongest climatic responses are seen in the parameters related to latewood cell-wall mass. The pattern for maximum density and the cell-wall proportion in latewood were most significant in response to climate. In this dataset previous year conditions were only of minor importance.

Cluster analysis (Fig. 7) showed a tree in which the leaves represent the measured tree-ring variables. The vertical coordinate of the place where two branches join equals the dissimilarity between the corresponding clusters. Latewood proportion separated

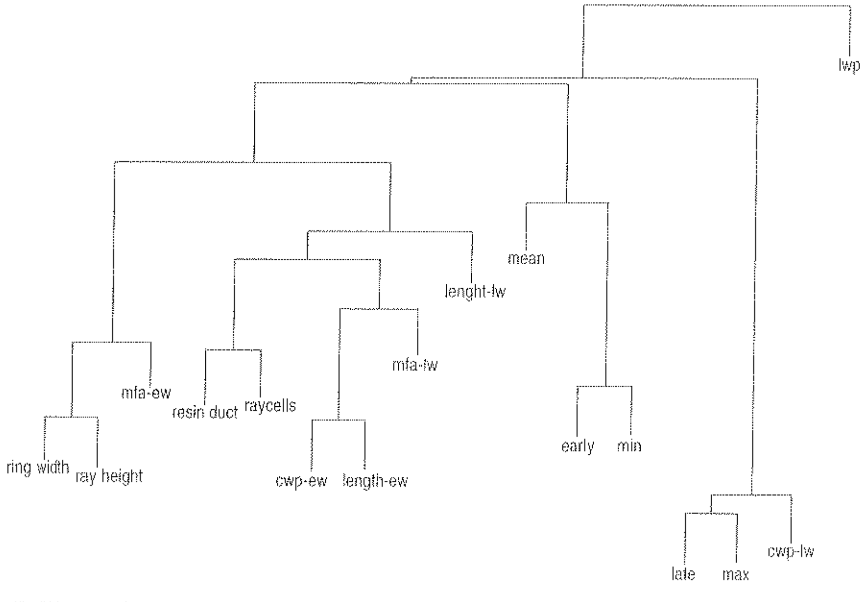


Fig. 7. Hierarchical clustering tree indicating the order in which groups were split or combined. See Figures 5 and 6 for abbreviations.

from all other measured features. The dendrogram then identified three major groups: 1) the latewood components and cell-wall proportion in latewood; 2) earlywood density features, mean ring density, and 3) all other variables. This third group included one subgroup encompassing ring width, ray height and earlywood microfibril angle, and a second subgroup that includes resin duct density, tracheid length, raycell number, cell-wall proportion in earlywood, and microfibril angle in latewood.

Table 1. Correlation coefficients (Pearson) among tree-ring parameters. Significance (two-tailed) at the 0.1when $r > 0.26$, or at the 0.01 level when $r > 0.40$, $n = 40$.

	Ring width	Latewood proportion	Mean ring density	Earlywood density	Latewood density	Minimum density	Maximum density	Resin ducts	Cell wall prop. earlywood	Cell wall prop. latewood	MFA latewood
Latewood proportion	-0.26										
Mean ring density	-0.33	0.26									
Earlywood density	n.s.	-0.42	0.55								
Latewood density	-0.23	-0.42	0.41	n.s.							
Minimum density	n.s.	-0.26	0.41	0.87	n.s.						
Maximum density	n.s.	-0.47	0.40	n.s.	0.97	n.s.					
Resin ducts	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.				
Cell wall prop. earlywood	n.s.	-0.30	n.s.	n.s.	n.s.	0.26	n.s.	n.s.			
Cell wall prop. latewood	-n.s.	-0.48	0.42	0.36	0.87	n.s.	0.95	n.s.	n.s.		
MFA latewood	n.s.	n.s.	n.s.	n.s.	-0.27	n.s.	-0.27	n.s.	n.s.	-0.29	
Ray height	0.29	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.30	n.s.	n.s.	n.s.

Tree-ring parameters do not respond to the environment independently; they rather are a complex interrelated system. Table 1 shows Pearson's correlation coefficients for features with at least one correlation significant. The raycell number, microfibril angle in earlywood and tracheid length (early- and latewood) were not correlated. As expected, maximum density had the strongest relationship to cell-wall proportion in latewood with $r = 0.95$ ($p < 0.001$) and to latewood density with $r = 0.97$ ($p < 0.001$). Minimum and earlywood density correlate with $r = 0.87$ ($p < 0.001$).

Resin duct density and ray height were negatively correlated ($r = -0.3$, $p < 0.05$). Microfibril angle in latewood did not correlate with tracheid length but with cell-wall proportion in latewood ($r = -0.29$). Ring width was weakly related to latewood proportion ($r = -0.26$, $p < 0.1$) and to mean ring density ($r = -0.33$, $p < 0.05$).

Table 2. Standardised path coefficients of tree-ring features estimating wood density components as dependent variables. Only ring features showing at least one significant path coefficient are listed. Significant coefficients ($p < 0.05$) are indicated bold. Explained variances are different from 0 with $p < 0.001$.

Dependent variables	Ring width	Latewood proportion	Cell wall prop. latewood	Latewood tracheid length	Explained variance R^2
Mean ring density	- 0.20	**+ 0.54**	**+ 0.73**	**- 0.22**	0.53
Earlywood density	- 0.09	**- 0.34**	+ 0.23	- 0.18	0.26
Latewood density	**- 0.25**	- 0.11	**+ 0.84**	- 0.10	0.83
Minimum density	- 0.17	**- 0.37**	- 0.14	**- 0.26**	0.21
Maximum density	**- 0.16**	- 0.09	**+ 0.91**	- 0.03	0.92

Table 2 lists standardised path coefficients for the measured wood density variables. This analysis showed that increasing ring widths had direct (negative) effects only on latewood density and maximum density. Latewood proportion correlated with several density components (Table 1) but had a direct positive relationship only with mean density and a weaker negative relationship with earlywood density components. According to these results, latewood proportion is independent from latewood density components. As expected, latewood cell-wall proportion had high path coefficients with maximum density as well as latewood density. Tracheid length measured in latewood showed a weak negative effect on density. Overall, maximum density was more or less identical with cell-wall proportion in latewood ($R^2 = 0.91$). Variation in latewood proportion, cell-wall proportion and latewood tracheid length explained 53% of the mean ring density.

DISCUSSIONS

Wood anatomical features measured in tree rings may offer opportunities for obtaining environmental information (Beeckman 1993). In many studies growth rate is the only considered parameter (e.g. Blasing & Fritts 1976; Till & Guiot 1990; Tessier et al. 1994; Szeicz 1997) since ring widths are usually easy to measure and to interpret. The current ring-width data show rather weak relationships with climate. Ring width depends mainly on the rate of periclinal cell division and the cell enlargement phase in the cambial region. The third phase in wood formations is cell-wall thickening which extends into late summer after cell division and enlargement have already ceased (Larson 1994). According to this model, growth limiting conditions taking place later in the season would not affect ring width.

Latewood proportion is positively correlated with summer rainfall. This could mean that above average rainfall during summer caused an early cessation of earlywood growth followed by a longer period of latewood formation. Denne (1979) observed an increase in the latewood proportion which was related to increased light intensity. Dietrichson (1964) proposed an association between earlywood–latewood transition and time of flushing. Trees that flush early may start to produce latewood earlier resulting in higher latewood proportions. However, trees might also continue to produce latewood later in the season and thus have higher latewood proportions. The results of this study better support the second hypothesis.

Density features measured in latewood have been used in numerous climatic studies (e.g. Conkey 1986; D'Arrigo et al. 1992; Luckmann et al. 1997; Briffa et al. 1998a, b) and in comparison with other tree-ring features densitometry has by far the highest potential for the extraction of environmental, particularly climatic information. Schweingruber et al. (1978) have successfully adapted microdensitometry – developed by H. Polge (Polge 1978) – as a significant method for dendroclimatological studies. Diaz-Vaz et al. (1975) report that densitometry correlates with the amount of cell-wall material which confirms the close relationship between latewood cell-wall proportion and maximum density. The obtained results again confirm the strong environmental significance of densitometric parameters, particularly of those measured in latewood. Temperature and precipitation in September were the most important variables affecting wood density. Rainfall was low in September (Fig. 2) thus limiting conditions during the latewood formation (Wodzicki 1971). During this growth period the cambium is most likely at the end of the cell-wall thickening phase of the very last formed tracheid rows. Therefore, an unusually warm September with low rainfall would lead to higher latewood densities as the tracheids accumulate more cell-wall material (Yasue et al. 2000).

Correlations between the other measured wood anatomical features and monthly temperatures and precipitation were not as strong as for wood density and cell-wall proportion, although some of the measured anatomical features showed significant relationships with temperature and precipitation. Anatomical features such as resin duct frequencies responded mainly to summer temperature, while ring widths were controlled mainly by precipitation (Wimmer & Grabner 1997). The obtained groups in the cluster analysis provide *a priori* information about the association of variables and confirm that density and cell-wall proportion measured in earlywood were widely independent from latewood, suggesting that they are not under the same control.

High latewood proportions are usually associated with higher wood density (Zobel & Van Buijtenen 1989), although the obtained correlations are not as high as with certain pine species (DeBell et al. 1994; Wimmer 1995). Path analysis showed that the positive link to latewood proportion is only true for mean density. Latewood proportion had a negative direct effect on density components of earlywood, and no direct effect on density components of latewood. But latewood proportions were correlated negatively to cell-wall proportion in latewood which had, in turn, a direct, strong and positive relationship to the latewood density components. Density variation in earlywood was explained through latewood proportion but not through cell-wall proportion in earlywood. It can be hypothesised that changing chemistry, i.e. lignin content, is responsible for this wood density change in earlywood. According to Wu & Wilson (1967) lignin content in earlywood is consistently 2 to 3% higher in earlywood than in latewood and the increased amount of less dense lignin might account for the earlywood density change to some extent. This needs to be verified through further research.

In conclusion, this study did not provide evidence that certain anatomical softwood features (e.g. tracheid length, ray cells, MFA) are strongly correlated to monthly climatic data, but did confirm previous findings that wood density components measured in tree rings are highly sensitive to climate (Park & Telewski 1993). Maximum density was more or less an identical measure for cell-wall proportion in latewood and therefore is a surrogate of cell morphological measurements performed through image analysis on microscopic sections.

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