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ORIGINAL ARTICLE

Variation of different tree-ring parameters in samples from each terminal shoot of a Norway spruce tree

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Abstract

Variability of wood parameters in a tree is sometimes a rather nebulous concept since variability is evident within single cells, from early to latewood, from pith to bark and from stem base to the top of a tree. So far, stem analyses have been done using a restricted number of parameters, mostly ring-width, and using a restricted number of samples in the longitudinal direction. This study analyses a number of parameters from a single tree. An 81-year-old spruce tree was felled and internodial discs were taken from each annual terminal shoot. All tree rings in each disc were measured and a whole-stem analysis was completed for the following parameters: ring-width, mean ring density, maximum density, percentage of latewood, type of transition from early to latewood, intra-annual density fluctuation, number of resin ducts per tree-ring and position of resin ducts within the tree-rings. All parameters showed calendar-year patterns, visible as lines parallel to the bark. The most clear calendar-year pattern was seen for the type of transition from early to latewood and for intra-annual density fluctuations. The strongest inter-series correlation between calendar rings was seen for ring-width. None of the parameters showed significant inter-series correlations for cambial rings. These results may help us to understand how cores or discs taken at breast height represent the entire tree.

Keywords: Whole-stem analysis; Tree-ring; Radial trends; Within-tree variation; Juvenile wood

Introduction

Wood structure varies greatly within trees, a fact that foresters and wood utilization researchers have been dealing with for a long time. Variation is evident within single cells, within tree-rings, from pith to bark and from stem base to tree-top (Wimmer, 1994). Most of the mechanical, anatomical and chemical characteristics follow consistent trends, with some varying only a few percentages, while others exhibit much higher variability. The large within-tree variation was expressed by Larson (1967) by quoting: "higher variability in wood characteristics exists within a single tree than among trees growing on the same site or between trees growing on different sites". The most discussed source of variation refers to the pith-to-bark trend, which is also called the juvenile–mature trend. A long-term downward trend in ring-widths with increasing age in many studies is called "age trend" (Fritts, 1976; Bräker, 1981; Krause, 1992; Krause and Eckstein, 1992; Abdel-Gadir and Krahmer, 1993).

Variation may also be considered in terms of genetic versus environmental effects, where the smoothed pith-to-bark trend reflects the underlying genetic potential of

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a tree on a given site (Abdel-Gadir and Krahmer, 1993; Yang et al., 1994; Downes et al., 1997). The scatter of points around a smoothed trend reflects the year-to-year variation in weather and climate – among the strongest driving factors in wood formation. The variability of certain wood structural parameters from pith to bark is exploited by dendrochronologists. Most parameters are determined on samples that are taken at breast height, disregarding the significant longitudinal variation within the stem (LeBlanc et al., 1987; Zobel and van Buijtenen, 1989; Wimmer, 1994).

Comparison of data from different heights within a stem (which may also include branches or even roots to some extent) is referred to as stem analysis. So far stem analyses have been done for a restricted number of parameters only, notably ring-width, with limited numbers of samples taken from several tree heights (LeBlanc et al., 1987; Kramer and Jiménez, 1991; Krause, 1992; Krause and Eckstein, 1992; Payette et al., 1996; Jiménez et al., 2003). Sampling heights were chosen either at fixed distances (Krause, 1992; Krause and Eckstein, 1992), or at percentages of the total tree height (Downes et al., 1997).

The purpose of this study was to undertake a complete tree analysis for a set of wood structural parameters by looking at every tree-ring, at every terminal internode. Complete tree images of parameters such as early to latewood transition, intra-annual density fluctuations and relative positions of resin ducts are shown for the first time. This qualitative and quantitative study is intended to improve our understanding of within-tree variability, the one of the most important biological basis of dendrochronology.

Material and methods

The sampling site was located in the Lachforst, Ranshofen, Upper Austria, approximately 60 km north from the city of Salzburg, an area located on a fluvial-terrace of the river Inn at about 380 m above sea level. The natural forest community is a submontane mixed oak–beech and oak–hornbeam type. The forests are dominated by even-aged conifers, mainly Norway spruce (*Picea abies* (L.) Karst.). The site was influenced by fluoride emissions starting 1947 and ending 1992 when the aluminium smelting plant was closed (Kisser et al., 1974; Baumann et al., 1989). One 81 years old, dominant spruce tree with a total height of 28 m and a straight, unbroken trunk with regular-shaped crown was selected. The sample tree was felled, cut into short logs and sawn into halves by cutting lengthwise near the pith, and finally into a series of thick radial boards. These boards were always orientated to the south-east and contained the pith. The tangential/longitudinal face of each board was carefully planned until the pith became visible. This procedure was necessary to accurately identify all internodes by visually assessing the winter bud of the terminal shoots. Annual height increments were measured as distance between neighbouring buds. From each terminal shoot we have cut discs 3 cm in thickness. In total, 81 sections were obtained which corresponded exactly with the number of rings on the disc taken from the tree base.

The dried discs were sanded with sandpaper up to 1000 grit until individual tracheids became visible. Tree-rings were measured to the nearest 0.01 mm using a LINTAB® measuring device (www.rinntech.de). All ring-width series were cross-dated (Swetnam et al., 1985; Stokes and Smiley, 1996) and checked for dating and measurement errors using COFECHA (Holmes, 1983), followed by a final visual check. On the sanded discs the different parameters were counted and measured along the radius from pith to bark in each tree-ring using a precision stereo-microscope equipped with a video-system. With this system it was possible to resolve clearly single tracheids. The type of transition from earlywood to latewood was visually assessed by splitting into the categories "gradual", "abrupt" and "compression wood", the latter judged by the shape, i.e. roundness of the tracheids and the entire ring structure. The appearance of intra-annual density fluctuations, i.e. false rings (Fritts, 1976), in earlywood and latewood was another visual parameter besides resin ducts, which were counted within a window that was demarked by the tree-ring radially, and 5 mm width tangentially. Resin ducts were categorized by their position within each ring: in earlywood, in the transition between early to latewood, in latewood or scattered across the ring. After measuring and counting at the polished surface, X-ray densitometry according to Lenz et al. (1976) was performed; this yielded the usual set of wood density parameters and the percentage of latewood. The analysis was done with the Walesch DENDRO 2003 equipment at the WSL, Birmensdorf, Switzerland.

For visualization (Fig. 1), the data were categorized and indicated with different grey-levels. Each square represents one tree-ring and each plot displays the complete tree-stem for a certain parameter. Missing values generally appear as empty squares. Vertical lines running parallel to the pith indicate cambial rings while tree-rings formed in the same calendar-year follow the diagonals parallel to the stem surface. To visualize the figures of each parameter determined at breast height, graphs of the 5th terminal shoot (1.35 m above ground) were plotted (see Figs. 4A–H).

A correlation analysis was performed to compare each internode using sequences of ten rings. The innermost 15 rings were excluded to minimize the juvenility effect. The decadal sequences were either aligned by their cambial rings (16–25) or by the same

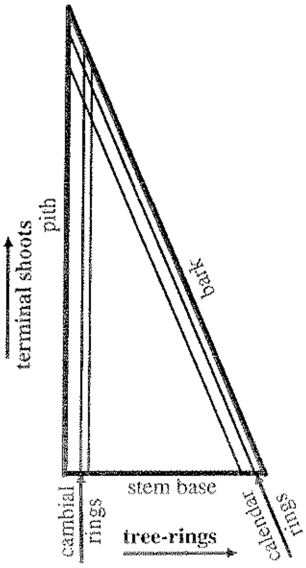

Fig. 1. Scheme illustrating the sampling concept with cambial rings vs. calendar rings varying along the radius and tree height.

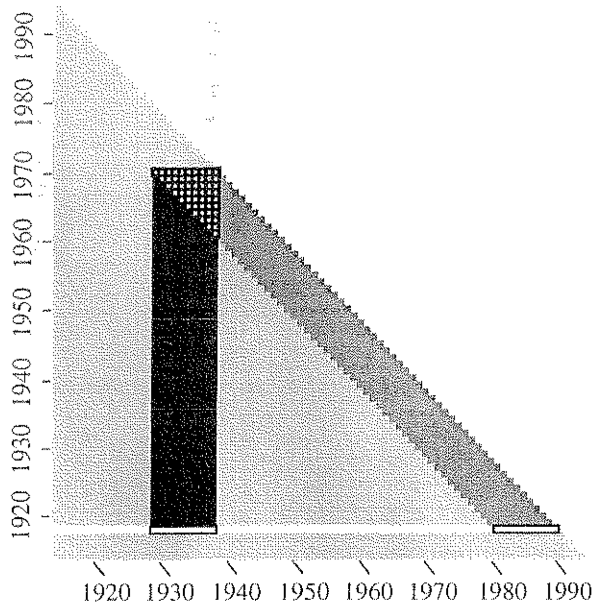

Fig. 2. Scheme of data arrangement of the simple correlation analysis (light grey = available data; white = 5th annual terminal shoot (1918; 1.35 m above ground), acting as reference; dark grey = data set of aligned calendar rings used in the analysis (10 tree-rings; 1985–1994); black = data set of aligned cambial rings used in the analysis (10 tree-rings; cambial rings 16–25)).

calendar-years (1985–1994; see Fig. 2). Correlations were calculated between the 5th terminal shoot (1.35 m above ground) and the terminal shoots above, up to the 56th terminal shoot. Significant coefficients of correlation ($p < 0.05$) are presented in Table 1. The mean values of all significant ($p < 0.05$) coefficients of correlations were calculated.

Results and discussion

Height increment of the terminal shoot

The annual shoot length varied between 2 and 91 cm (mean value: 34 cm). There is a strong yearly variation in height increment (Fig. 3), which was also described by Pensa et al. (2005). A decreasing trend of height increment with increasing age is visible.

Ring-width

Ring width varied between 0.3 and 10.3 mm (mean value: 2.6 mm), but there was no distinct trend with age (Fritts, 1976; Bräker, 1981; Fig. 4A). The ring-width pattern did not show a sharp demarcation between juvenile wood and mature wood. The period of accelerated growth (1925–1946) exhibited an age trend in the lower portion of the stem, i.e. from the base up to the annual terminal shoot of 1946. The ring-width pattern of the investigated spruce tree did not match well with concepts described in the literature, such as the one by Payette et al. (1996), who proposed the existence of a cylinder of higher juvenile growth along the terminal shoots, or the conical juvenile wood core model of Yang et al. (1994).

The growth reduction after the aforementioned period of rapid growth (1925–1946) may be caused by severe fluoride air pollution at the end of the Second World War. The pattern of narrowing tree-rings at the outermost part is clearly associated with a common set of calendar-years along the terminal shoots. Krause (1992) mentioned that characteristic tree-rings are not only visible along the stem, but also in tree-rings of branches and roots. Strong correlations between the internodes were found for the characteristics of wood produced in the same calendar-years (mean value of all significant coefficients of correlations; $r = 0.78$, ranging from 0.64 to 0.98), but no significant relationships were found using a cambial ring basis (Table 1). This confirms the strong impact of climate on wood formation as described in the literature (e.g., Fritts, 1976; Schweingruber, 1983).

Mean ring density

Mean ring density varied between 0.27 and 0.92 g/cm^3 (mean value: 0.47 g/cm^3). The fast-growing period (1925–1946) is associated with lower density (Fig. 4B). The outermost tree-rings show higher mean ring densities, as frequently reported in literature (e.g.,

Table 1. Coefficients of inter-series correlation (r; $p < 0.05$) between the 5th terminal shoot and the shoots above for calendar and cambial rings. Only significant values are shown

Shoot no	Year	Ring-width		Mean ring density		Maximum density		Latewood perc.	
		Calender	Cambial	Calender	Cambial	Calender	Cambial	Calender	Cambial
57	1970					0.65			
56	1969								
55	1968								
54	1967								
53	1966	0.73							
52	1965								
51	1964	0.66				0.72			
50	1963	0.78							
49	1962								
48	1961								
47	1960								
46	1959								
45	1958								
44	1957	0.70				0.76			
43	1956								
42	1955	0.68				0.68			
41	1954	0.72							
40	1953	0.74							
39	1952								
38	1951								
37	1950								
36	1949								
35	1948								
34	1947								
33	1946								
32	1945								
31	1944								
30	1943								
29	1942								
28	1941								
27	1940								
26	1939								
25	1938								
24	1937								
23	1936								
22	1935	0.64							
21	1934	0.71							
20	1933								
19	1932								
18	1931								
17	1930	0.65							
16	1929								
15	1928	0.65							
14	1927	0.65				0.77			
13	1926					0.64			
12	1925	0.82							
11	1924	0.92							
10	1923	0.94							
9	1922	0.90		0.69		0.67			
8	1921	0.93		0.72		0.77		0.71	
7	1920	0.98		0.68		0.65		0.91	
6	1919	0.98		0.83		0.70		0.87	

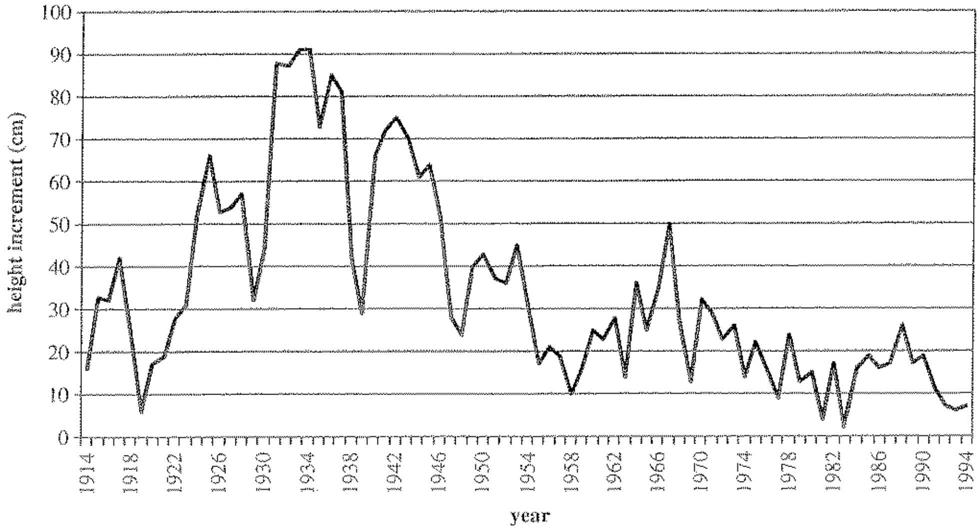

Fig. 3. Annual height increment (cm) of the terminal shoot.

Kollmann, 1951; Göhre, 1958; Bosshard, 1974; Panshin and De Zeeuw, 1980). There are several terminal shoots (1928, 1942–1944) with a generally higher wood density visible as horizontal lines. No definite explanation can be given for this pattern but one might hypothesize that this is related to stem straightness defects, i.e. sinuosity, which is stem waviness or crookedness totally within inter-whorl segments (Doede and Adams, 1998; Temel and Adams, 2000). This phenomenon is most common in Douglas-fir but has not been seen in spruce. It is likely to signify a type of mechanical stabilization response of the tree. The wood formed higher up in the stem seemed to have slightly higher wood density. The effect of rapid growth from 1925 to 1946 and the horizontal regions of higher density in this tree mask possible radial trends in wood density as described in Bräker (1981) and Abdel-Gadir and Krahmer (1993). Zobel and van Buijtenen (1989) indicated that wood density may initially decrease with age close to the pith, before rising as the wood approaches maturity. These authors also reported slight changes in wood density with height for spruce, while Mitchell and Denne (1997) did not see such a trend.

An expected inverse correlation between ring-width and mean ring density was evident but not strong. Downes et al. (2002) stated that growth pattern and not the rate of growth is the main cause of variation. They claim that the pattern of variation of mean ring density is more strongly related to the percentage of latewood than to ring-width. This strong relationship was confirmed by Wimmer and Grabner (2000). In the current study, correlation analysis has shown lower r-values for mean ring density than for ring-width (calendar rings mean $r = 0.73$, ranging from 0.68 to 0.83; no significant relationships within cambial rings; Table 1).

Maximum density per tree-ring

Maximum latewood density varied between 0.54 and 1.42 g/cm^3 (mean value: 0.92 g/cm^3). The aforementioned fast growing period (1925–1946) is not visible for the maximum density (Fig. 4C). The radial trend of maximum density was an expressed increase in the first decades, followed by a flattening out and stable trend for the higher age period, as described by Bräker (1981) and Abdel-Gadir and Krahmer (1993). The base of the stem had generally lower maximum density values. The horizontal lines (rows of similar grey level), in the mean ring density tree map (Fig. 4B: 1928, 1942–1944) are also visible in the maximum density map. Maximum density and ring-widths showed similar results for the correlation analyses – high values for calendar-years (mean $r = 0.71$, ranging from 0.65 to 0.82), and no significant results for cambial rings (Table 1).

Latewood percentage

The percentage of latewood varied between 4% and 94% (mean value: 31.6%). The very high percentages of latewood were associated with compression wood (Fig. 4D). To visualize the amount of latewood, compression wood was not excluded from the analysis. High percentages of latewood corresponded with visually assessed compression wood (Fig. 4E) with few exceptions (for example 1951 and 1953). Up to the age of about 30 years, the tree contained relatively low proportion of latewood (Fig. 4D). The horizontal lines as seen in the mean ring density and maximum density tree maps are also evident in the percentage of latewood map. With increasing age, the percentage of latewood increased, and this was also reported by Bräker (1981) and Wimmer (1994). Because of the distinct calendar-year pattern, the influence of climate on the percentage of latewood is evident. The reasons for the onset of latewood formation is debated, however possible influencing factors – including climate – are summarized in Zobel and van Buijtenen (1989). The correlation analysis showed a low number of significant relationships across stem heights for calendar-year rings, and no significant results for cambial rings (Table 1). The coefficients of correlation calculated for the calendar-year rings decreased with increasing distance from the reference height.

Early to latewood transition

Transition from earlywood to latewood appeared to be mainly gradual (Fig. 4E), as found in earlier studies (Liese and Dujesiefken, 1986). However, some years clearly showed abrupt transitions throughout the stem. This may be indicative of a strong effect of climate. Krause (1992) reported relationships between abrupt earlywood–latewood changes and strong temperature fluctuation, in combination with drought periods in spring and early summer. Compression wood was found in the innermost tree-rings along the stem, distinct from the juvenile wood. Zobel and

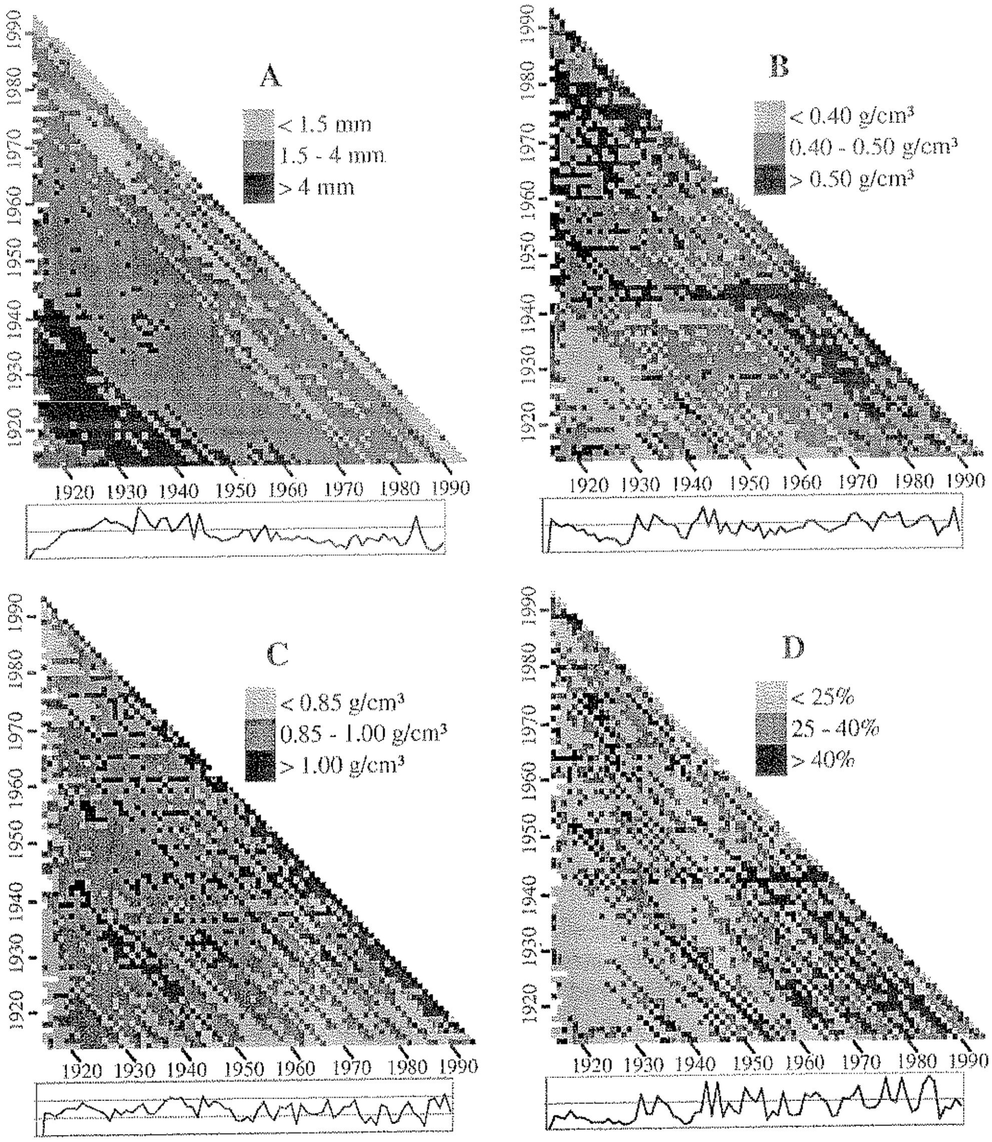

Fig. 4. Ring-wise data of: A – ring-width (grouped); B – mean ring density per tree-ring (grouped); C – maximum density per tree-ring (grouped); D – latewood percentage (grouped); labelled in different grey levels. The graphs of the 5th annual terminal shoot (1918) are given beyond. Ring-wise data of: E – early to latewood transition; F – intra-annual density fluctuations; G – number of resin ducts per tree-ring (grouped); H – relative position of resin ducts; labelled in different grey levels. The graphs of the 5th annual terminal shoot (1918) are given beyond (cw: compression wood; a: abrupt; g: gradual; df: density fluctuation; s: scattered; lw: latewood; t: early latewood transition; ew: earlywood).

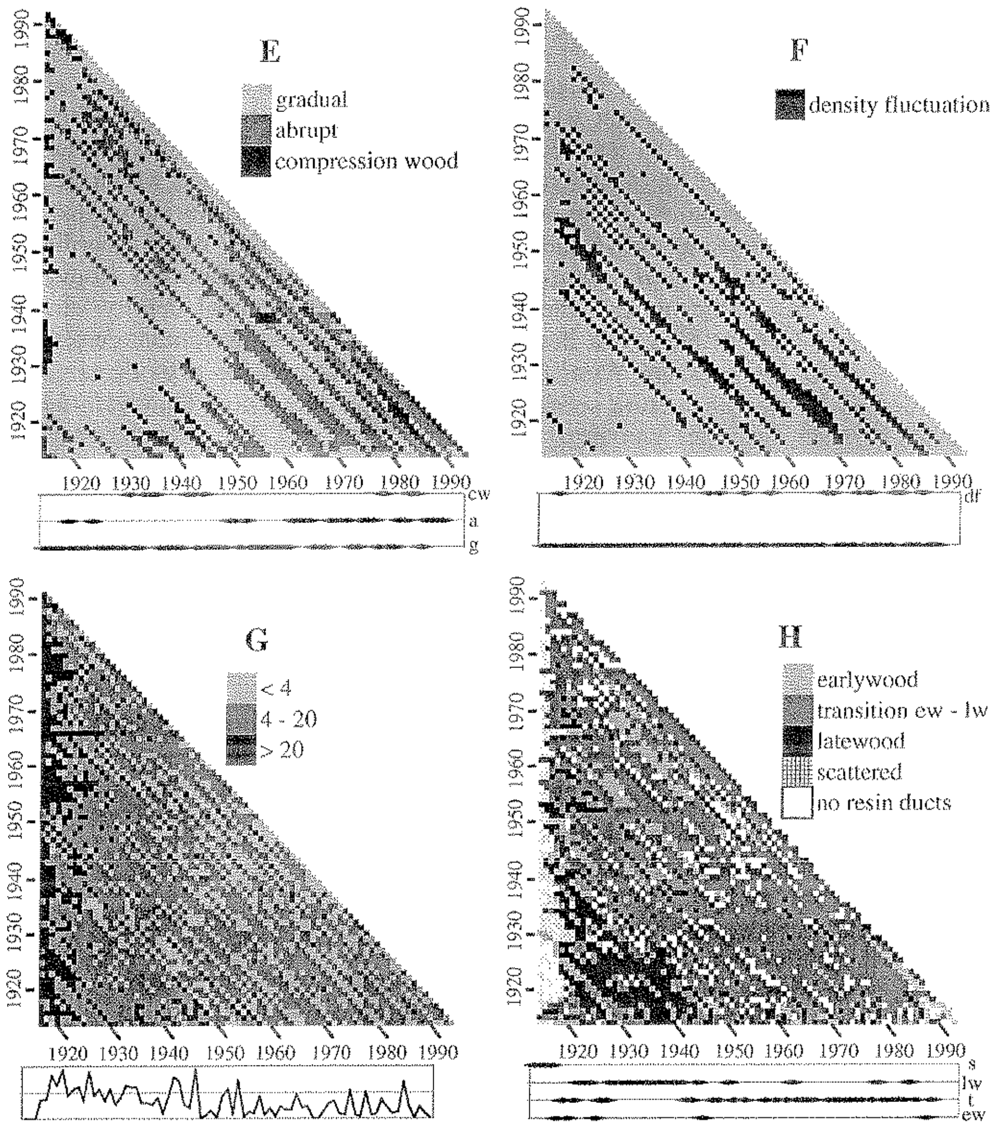

Fig. 4. (*Continued*)

van Buijtenen (1989) have described such associations between juvenile wood and reaction wood. The 1990 tree-ring was found to be mostly compression wood in all annual terminal shoots. Severe clear-cutting activities during the previous winter next to the site (personal communication of the foresters) could have induced compression wood formation. Between 1935 and 1949 four years showed clear compression wood formation in the lower part of the stem. This phenomenon may be attributed to a period of mechanical adjustments of the tree.

Intra-annual density fluctuations

Density fluctuations were strong in certain calendar years and extended through many internodes of the stem (Fig. 4F). No density fluctuations were seen in the juvenile wood zone. Between the years 1925 and 1946, a period with higher growth rates, no intra-annual density fluctuations were visible (Fig. 4F). Krause and Eckstein (1992) have looked at tree-rings formed in stems, roots and branches of different tree species and found intra-annual density fluctuations appearing throughout the tree. Krause (1992) described climate conditions leading to density fluctuations in spruce trees: type 1 refer to warm and dry summers, type 2 to dry springs and temperature abnormalities in summer. Rigling et al. (2001) summarized possible climate abnormalities as driving factors for intra-annual density fluctuations, and Wimmer et al. (2000) found strong linkages between spring drought and intra-annual density fluctuations in Austrian pine.

Resin duct numbers

The number of resin ducts within tree-rings ranged between 0 and 115 (median 8.0) within a 5 mm wide tangential window (Fig. 4G). In general, high numbers of resin ducts were evident within the first 10–14 cambial rings, which was a clear factor of juvenility. No clear trend was seen with age (radial direction). Resin duct numbers varied substantially from year to year, but also exhibited clear relationships with particular calendar-years. Examples are 1950 and 1956 for high resin duct numbers, and 1966 and 1980 for low numbers. Wimmer and Grabner (1997) demonstrated with mature spruce trees that the number of resin ducts per unit area is positively linked to summer temperatures. Levanic (1999) was not able to confirm these findings for black pine grown in Slovenia. The current study shows that rings with high numbers of resin ducts appear throughout the stem, indicating that external factors such as climate might be more relevant than local impacts such as wounds.

Relative position of resin ducts

A strong juvenility effect was also seen in the relative positions of resin ducts in tree-rings. While the innermost tree-rings showed resin ducts scattered over the whole tree-ring (Fig. 4H), the preferred location in mature wood was the transition between earlywood and latewood. This confirms the finding by Reid and Watson (1966) that resin ducts in Lodgepole pine form during the latter half of the growing season. Schweingruber (2001) also stated that resin ducts in Siberian larch, stone pine and spruce are normally located in latewood, and in the transition zone between earlywood and latewood. Within the period of rapid growth (1925–1946) resin ducts were located more in the latewood than in the transition zone. The white squares in Fig. 4H represent tree-rings with no observed resin ducts. These resin duct free tree-rings are associated with particular calendar years all the way down the stem, and may be associated with mild summer conditions with moderate temperature and no drought periods (Wimmer and Grabner, 1997). Wimmer et al. (1999) reviewed the literature concerned with the number and position of resin ducts. Only a few studies focus on these topics, making comparisons difficult. Generally, vertical resin ducts are more likely to be confined to the latewood in pines than in spruce (Wimmer et al., 1999).

Demarcation of juvenile wood

For all the described parameters of this single spruce tree no common geometry was associated with the juvenile wood zone. Downes et al. (1997) extended earlier findings of Evans et al. (1995) and described four possible patterns of variation, mapped onto conical shapes: cylindrical symmetry, conical symmetry, general linear and general non-linear. The strongest effect of juvenility was seen for resin ducts, i.e. resin duct number per tree-ring and position within tree-rings. Resin ducts showed a pattern of variation that matched with the cylindrical-symmetry-model according to Downes et al. (1997). All other parameters (transition from early to latewood, intra-annual density variations, ring-width, mean ring density, maximum density and percentage of latewood) showed no clear demarcation between juvenile and mature wood. However, these parameters were strongly aligned with calendar-years along the annual terminal shoots as described by the conical-symmetry-model. Abdel-Gadir and Krahmer (1993) summarized: "The change from juvenile wood to typical mature wood is neither sharp nor the same for all intra-ring characteristics."

Evaluating sampling strategies

In dendrochronological studies the usual sampling position is breast height (Schweingruber, 1983). To evaluate the significance of this sampling point a correlation analysis was performed. The ring-width pattern of the 5th annual terminal shoot (1.35 m above ground) showed significant correlations with the ring-widths of the internodes above, if aligned by calendar years (see Table 1). Averaging the significant correlation coefficients of the 52 terminal shoots above the reference (5th terminal shoot) by calendar rings resulted in $r = 0.78$ (ranging from 0.64 to 0.98). The lower terminal shoots were excluded from the analysis because of expected influences of the root system on ring-width below breast height. The results of the calendar ring comparisons were: for mean ring density $r = 0.73$ (ranging from 0.68 to 0.83), for maximum latewood density $r = 0.71$ (ranging from 0.65 to 0.82), and for the latewood percentage $r = 0.83$ (ranging from 0.71 to 0.91) with just three significant results. It can be concluded that cores taken at breast height represent the annual pattern of the whole stem for major dendrochronological parameters (ring-width and maximum latewood density).

In wood quality studies measurements are often done at defined tree ages (cambial ring number). The correlation coefficients for the cambial rings, averaged across the 52 terminal shoots above the reference, were all non-significant. Climate (calendar-year rings) had a higher impact on ring pattern than did cambial age, as discussed in the literature (e.g., Fritts, 1976; Bräker, 1981; Schweingruber, 1983). Therefore, owing to the different pattern for each of the parameters, no general recommendation for an optimal sampling point to study wood quality can be given.

Conclusions

A whole-stem analysis using each terminal shoot is helpful in visualizing the variability within a stem. Dendrochronologists looking for the sample that represents best the climate–growth relationships, as well as those who are looking for the best way to represent wood quality in the entire tree, may learn a great deal about within-tree variability from such whole-stem analysis. The parameters studied here showed different trends with age. It was not possible to determine a general pattern for juvenile–mature wood demarcation that would be valid for all observed parameters.

To answer the questions of optimum sampling points, breast height remains a good choice for dendrochronologists, as it encompasses almost all available tree-rings and most of the year-to-year variations. For wood quality studies there is no general recommendation for the best sampling point as it depends on the parameter investigated.

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