INTRODUCTION

Resin ducts are normal features of the wood and bark of many conifers, particularly of *Pinus*, *Picea*, *Pseudotsuga* and *Larix* (Fig. 5.1, LaPasha and Wheeler, 1990). These species develop resin ducts axially as well as horizontally, forming an interconnecting system, the extent of this system varying between genera. In addition, wounding (pressure wounds, frost, wind) may result in the formation of traumatic resin ducts, even in *Abies* or *Tsuga* where ducts are not present in healthy tissues, giving the potential for further resin production in the injured area. Resin ducts never occur in the wood of some conifers, e.g. *Juniperus* and *Cupressus* (Fahn and Zamski, 1970). The duct diameters are largest in *Pinus* species (60–300 µm) and smaller in *Larix* (40–80 µm), *Picea* (40–70 µm) and *Pseudotsuga* (40–45 µm) (Larson, 1994). Both vertical and radial resin ducts are found in these genera, and both types occur in traumatic as well as normal duct systems.

The frequency of resin ducts in tree rings, their position within tree rings and their horizontal and vertical variability within a tree are poorly investigated. Reid and Watson (1966) report that vertical ducts form during the latter half of the seasonal growth period. According to their results, resin ducts are located mainly in the latewood portion of tree rings. For lodgepole pine it was found that 88% of the resin ducts are in the last 40% of the tree ring. But number and position of vertical resin ducts might also be influenced by external conditions (Wodzicki, 1961; Larson, 1994). In a laboratory experiment using 2-year-old *Pinus halepensis* Mill., Zamski (1972) showed that temperature and photoperiod changes influence resin duct formation with a time lag of several months. The study also proved temperature to be of higher importance than the photoperiod.

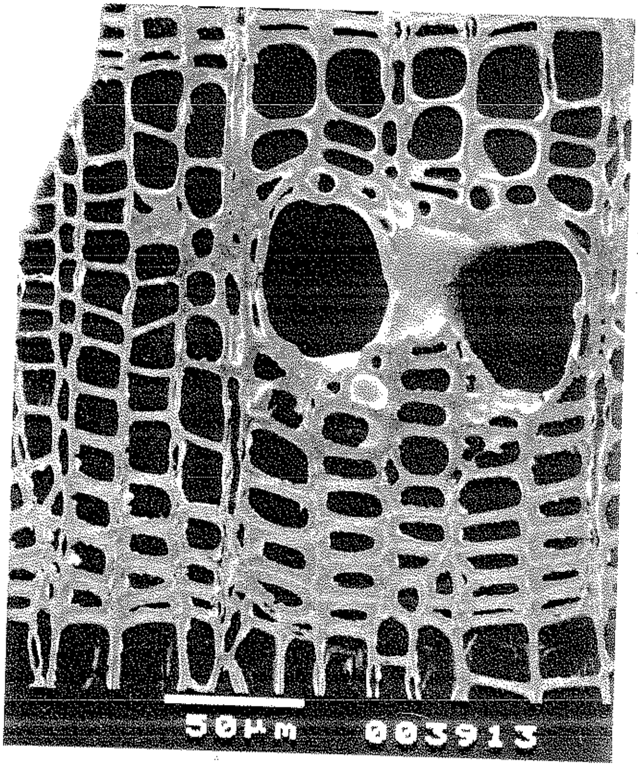

Fig. 5.1. Cross-sectional SEM-image of vertical resin ducts in a spruce tree ring.

Ruden (1987) measured ring width and resin duct frequencies in Scots pine and was able to show that both variables are related to climatic data. Wimmer and Grabner (1997) demonstrated with mature spruce trees that the number of resin ducts per unit area in tree rings is positively linked to summer temperatures. The current study presents two new aspects of resin ducts in spruce tree rings: first, a complete resin duct stem-analysis and, second, the periodicity of resin duct series.

MATERIAL AND METHODS

The first sampling site is located in the 'Lachforst', Ranshofen, Upper Austria, approximately 60 km north from the city of Salzburg, Austria. The site is located on a fluvial-terrace of the Inn River at about 380 m a.s.l. The natural forest community is submontane mixed oak–beech and oak–hornbeam. The actual forests are dominated by even-aged conifers with spruce as the dominant species. At this site, one mature spruce tree (*Picea abies* (L.) Karst.) with a straight, unbroken trunk and a regular-shaped crown was selected. The sample tree was felled in January 1995 and the stem was cut into pieces and sawn into halves by cutting lengthwise through the pith. This procedure was necessary to accurately identify all terminal shoots. From each terminal shoot, disc sections were cut with a chain saw. In total, 84 sections were obtained which corresponded with the number of rings on the disc taken from the base of the tree. The discs were sanded using conventional sandpaper ranging from 100 to 1000 grit. On the sanded discs the resin ducts were counted along radii in each tree ring using a regular stereo-microscope equipped with a video-system. With this procedure it was possible to resolve clearly single tracheids.

The numbers were related to an area that was obtained by multiplying the given tangential window by the ring width, resulting in the parameter 'resin duct density'. In addition, the relative positions of the resin ducts within the tree rings were determined by using the five-step ordinate scale: initial, earlywood–latewood transition, latewood, terminal and dispersed.

The second site is located in the forest district Seyde, Eastern Erzgebirge, about 50 km south of Dresden in Germany, close to the Czech border. On this site, even-aged and approximately 80-year-old Norway spruce trees were sampled. The natural forest community is a mixed beech–fir–spruce forest at a maximum altitude of 800 m a.s.l. Spruce trees cover 80% of this area and on the quartz-porphyric bedrock the predominant brown soils are partially podzolized. In April 1993, 20 dominant and codominant trees were felled and 5-cm-thick stem discs were removed at the 1 m tree height. Discs were transported to the laboratory for the preparation of continuous series of blocks from pith to bark. Transverse sections 20 μm thick were cut from these blocks using a sledge microtome and sections were dehydrated, stained with methylene blue and mounted permanently in Malinol on slides (Gerlach, 1984). The tree rings formed between 1941 and 1987 were analysed. Three radii facing to north, south and east were prepared from each disc and sections were observed through a transmitting light microscope with a CCD-camera connected to a standard video system. Resin ducts were counted in each individual ring from pith to bark. Numbers were also related to an area that was obtained by multiplying the given tangential window by the ring width. We tried to differentiate between regular and traumatic resin duct formations and excluded the latter from the investigation. The final resin duct density is substantial and contains 58 series.

The Eastern Erzgebirge is located in a transition from atlantic to continental climate types. This area experiences especially high fluctuations in temperature with cold winters and little precipitation. Total annual precipitation for these sites is 965 mm, 38% of which is snow. Annual mean temperature is 5.5°C, with −23°C as the lowest temperature measured. Homogenized climatic data representative for the Seyde area were used (Deutscher Wetterdienst, Wetteramt Dresden).

Samples from both sites were crossdated according to the procedure outlined in Swetnam *et al.* (1985) and ring widths were measured to the nearest 0.01 mm using a regular incremental measuring machine. Data were further checked for dating and measurement errors using COFECHA (Holmes, 1983). Figure 5.2 demonstrates that the parameters resin duct density and ring widths are independent and Fig. 5.3 illustrates that ring widths generally follow a negative exponential curve while resin duct density trend is basically linear. Therefore, the resin duct data set from the Erzgebirge site was not detrended, only a horizontal line was fitted through the mean. To investigate the frequency properties of the resin duct density series over time, a spectral analysis was performed using the SPSS (1997) computer software. With a power spectral analysis the variance of each wavelength is estimated through a Fourier transformation of the autocorrelation function (Fritts, 1976).

RESULTS AND DISCUSSION

Resin Duct Stem Analysis

The resin duct densities are shown in Fig. 5.4a. In total, 3280 tree rings are included in each figure. Two trends can be extracted from the tree. First, the resin duct densities for each year are averaged and plotted in Fig. 5.5. Second, the series are sorted by their cambial age and re-plotted in Fig. 5.6. Particular years show extremely high resin duct densities, such as the dry year 1976 (Figs

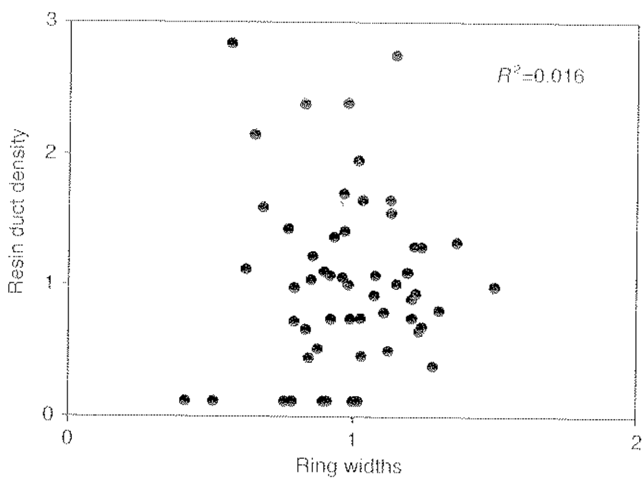

Fig. 5.2. Scatterplot of ring widths and resin duct density. There is no significant relationship between these two parameters.

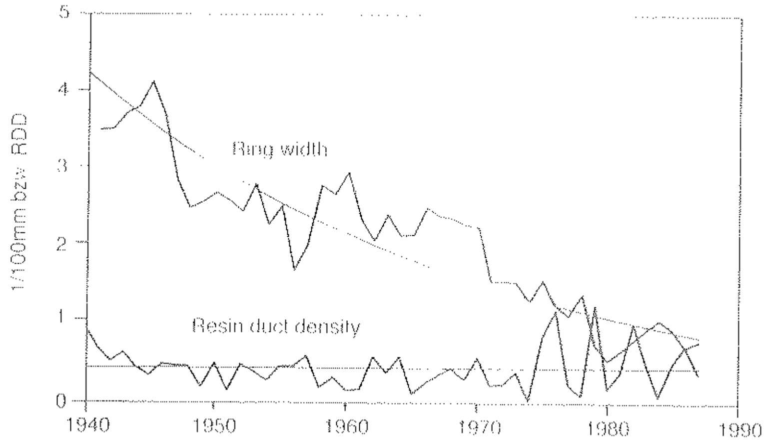

Fig. 5.3. Radial trends of ring widths and resin duct density. Ring widths follow basically a negative exponential curve while resin duct density follows a nearly horizontal line through the mean.

5.4a and 5.5). These years show continuous bands along the stem. Other years have low resin duct densities, which might be due to regionally favourable climatic conditions. Figure 5.6 shows the trend caused by cambial ageing. The 10 years around the pith have numerous resin ducts (Fig 5.4a). Tree rings with a cambial age above 10 show a slight but constant increase for resin duct density. Trendelenburg and Mayer-Wegelin (1955) have already reported such an increase of the proportion of resin ducts from pith to bark.

Results for the relative positions of resin ducts are shown in Fig. 5.4b. According to this figure the majority of the resin ducts are located in the transition between earlywood and latewood. In Fig. 5.7 the 'position' trends averaged over the tree height through time are shown. In the early part, 1930–50, resin ducts are more likely to occur in the latewood, but since 1950 they fluctuate around the earlywood–latewood transition. In Fig. 5.8 the resin duct positions are plotted against their cambial age and this figure is showing basically the same tendency: the resin ducts in tree rings of young cambial age are more likely in the latewood, then they stay constant in the earlywood–latewood transition up to an age of 60 years, and then shift later slightly towards the earlywood. From Fig. 5.4b it can be seen that higher up in the stem resin ducts are located more frequently in earlywood. Comparisons with literature are difficult because only a few reports were focusing on the position of resin ducts in coniferous trees. A general statement was made by Reid and Watson (1966) mentioning that vertical resin ducts are located preferentially in the latewood of tree rings. Their results were based on young experimental trees. In mature spruce tree rings the position of resin ducts is most likely the

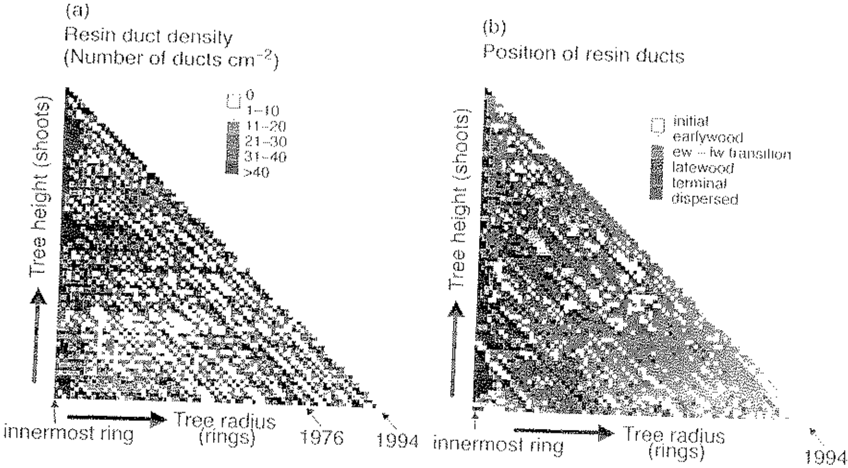

Fig. 5.4. Resin duct patterns showing the variation within the stem. (a): Resin duct density (unit: resin ducts cm^{-2}), (b): Resin duct position within tree rings (ordinate scale).

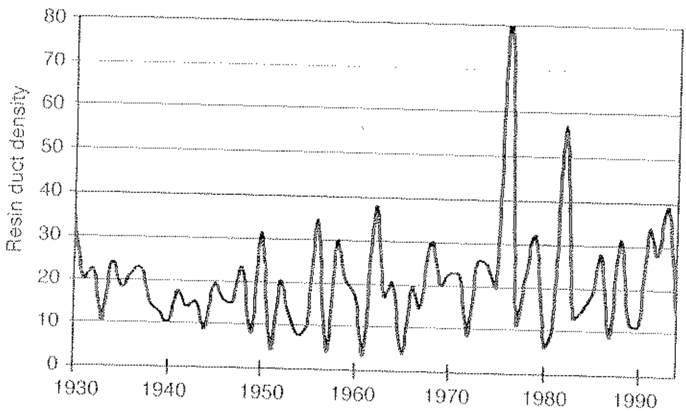

Fig. 5.5. Radial profile of resin duct density (unit: resin ducts cm^{-2}). The curve is an average over all profiles measured in each annual shoot.

transition from earlywood to latewood. Due to environmental stresses that occur earlier in the season, resin ducts could be formed even in the quickly differentiating earlywood. Werker and Fahn (1969) and Fahn (1979) found resin ducts concentrated mainly in the earlywood–latewood transition whereas

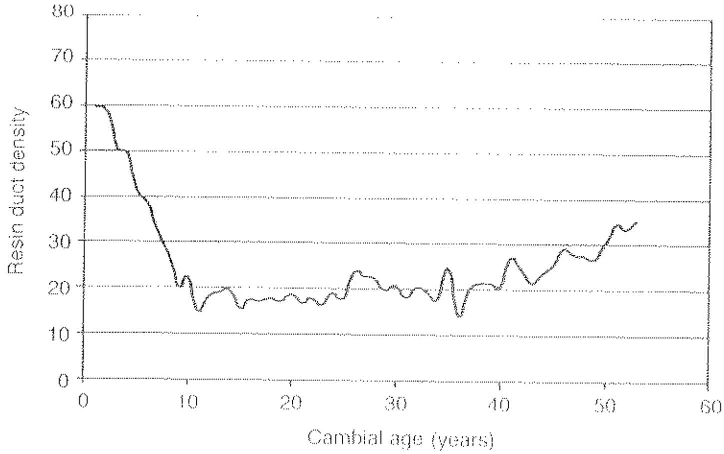

Fig. 5.6. Resin duct density profile and cambial age. The curve is an average over all profiles measured in each annual shoot sorted for their cambial age.

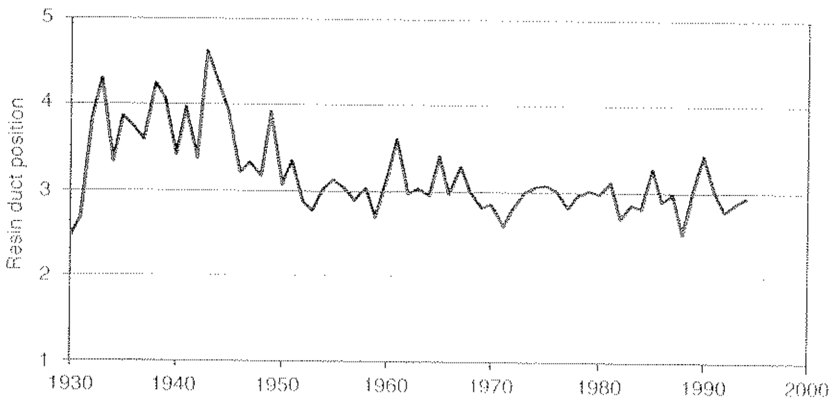

Fig. 5.7. Resin duct position profile. The curve is an average over all position profiles determined in each annual shoot. Relative duct position scale: 1 = initial, 2 = earlywood, 3 = transition earlywood–latewood, 4 = latewood, 5 = terminal.

Stephan (1967), Alfieri and Evert (1968) and Zamski (1972) concluded that resin ducts are concentrated in the latewood. A review of the literature gives the impression that vertical resin ducts are more likely to be confined to the latewood in *Pinus* than in *Picea* and *Larix*.

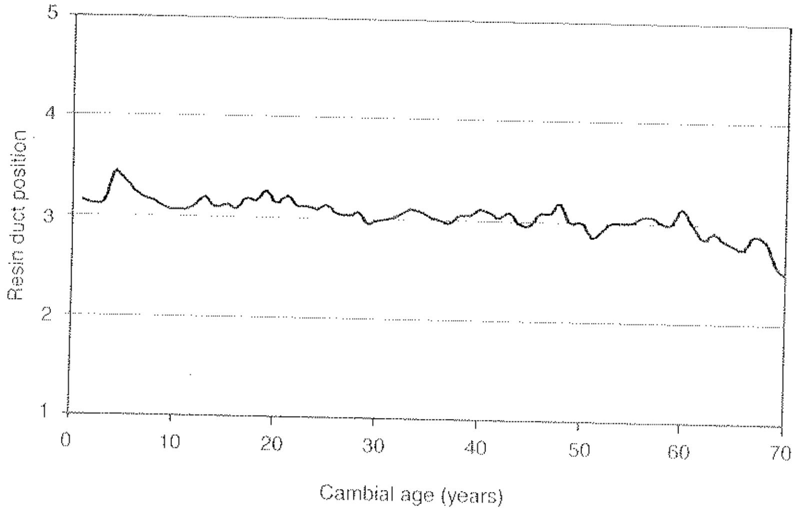

Fig. 5.8. Resin duct position profile and cambial age. The curve is an average over all position profiles determined in each annual shoot which were sorted by their cambial age. Relative duct position scale: 1 = initial, 2 = earlywood, 3 = transition earlywood–latewood, 4 = latewood, 5 = terminal.

Periodicity and Climate Signal in Resin Duct Series

The Erzgebirge data set with 58 resin duct series coming from 20 spruce trees was analysed earlier by Wimmer and Grabner (1997). Resin duct density data were symmetrically distributed with relatively high mean sensitivity and standard deviation but lower signal-to-noise ratio than the corresponding growth rate. The power spectrum analysis estimates the variance of each wavelength (power) and expresses it as a continuous distribution of wavelength throughout the entire spectrum. Figure 5.9 shows a peak at a period of approximately 3 years, which means that the resin ducts behave like a sine wave at this period length. This basic wavelength seems to be the only significant one as no other peak at wavelengths corresponding to one or more higher harmonics of the basic wavelength are seen.

In the previous study (Wimmer and Grabner, 1997), a correlation analysis between monthly climatic data and resin duct density in tree rings showed significant positive relationships with June and July temperature of the current year. In contrast, ring width showed a significant negative response to above-normal precipitation from June to August but no response with temperature. This was also found by others such as Reid and Watson (1966) who suggested circumstantial evidence for a direct relationship between high summer temperatures and large numbers of vertical ducts. Ruden (1987) used resin duct

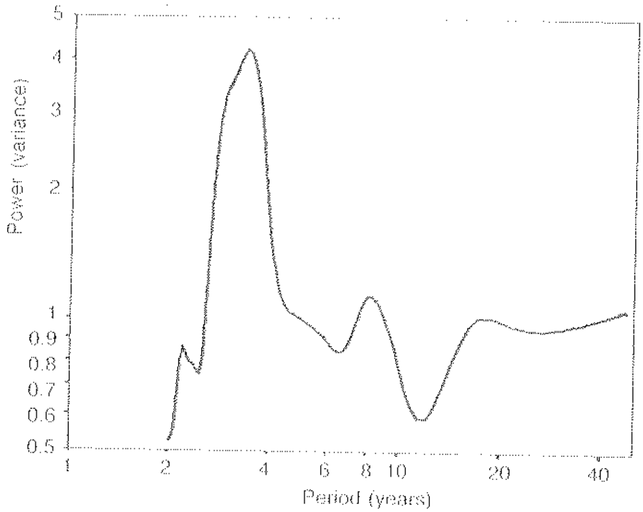

Fig. 5.9. Result of power spectra analysis of resin duct density series from the Erzgebirge (58 series from 20 trees). The maximal peak is at an approximately 3-year period.

frequency and ring width of seven old Scots pines to reconstruct climate for a certain period. He also found resin duct frequency correlated highly with summer drought.

In a cross-power spectrum analysis, the covariance expressed in the frequency domain between the resin duct series and the June–July temperature was computed. Coherency curves are obtained as a measure of similarity between the two series at each frequency. In Fig. 5.10 the highest coherency of 0.8 is at a period of about 3 years, which indicates that there is a causal relationship between resin ducts and summer temperature. A smaller peak can be seen at around 12 years (coherence = 0.6). Most spectral analyses in past dendrochronological research have dealt with radial increment as, for example, Stockton (1975), Fritts (1976), Stahle and Cleaveland (1988), Cook and Kairiukstis (1990) and Cook *et al.* (1998). Time series of various tree-ring parameters (density, anatomical features, ...) should be investigated for their frequency domain as an insight into biological and statistical relationships with regard to possible periodicities of factors controlling tree growth.

CONCLUSIONS

This study deals with two aspects of resin ducts in tree rings. First, a resin duct stem analysis demonstrates the within-tree variability and the effects of

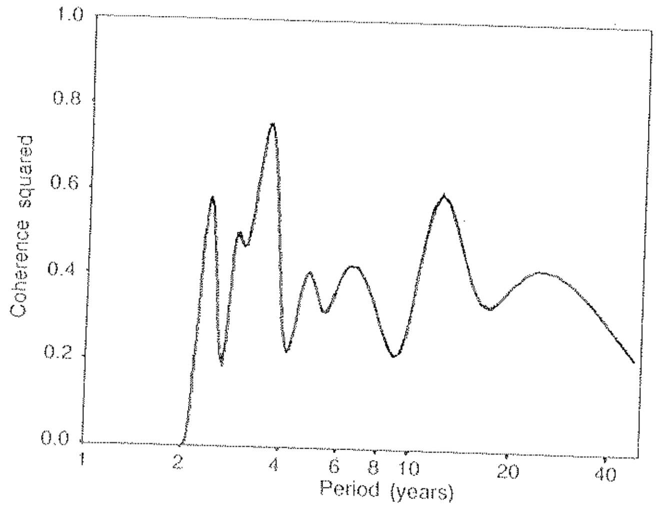

Fig. 5.10. Result of cross-power spectra analysis (coherence (= analogous to R^2) spectra) for resin duct density from the East Erzgebirge, Germany (58 series from 20 trees) and June/July temperature means.

cambium age on resin duct density. Second, the periodicity of resin duct series are explored statistically using a set of samples extracted from 20 spruce trees. The parameter 'resin duct density' is independent of ring width. Particular years show extreme high resin duct densities, such as the dry year 1976, and these years show continuous bands throughout the stem. Tree rings with a cambial age above 10 years show a slight but constant increase in resin duct densities. The majority of the resin ducts are located at the transition between earlywood and latewood. The resin ducts of tree rings at young cambial age are more likely to be in latewood. Summer temperature affects the formation of vertical resin ducts most. At a high frequency of about 3 years in the resin duct series a causal relationship can be seen with summer temperature. The current results should encourage researchers to investigate vertical resin ducts in tree rings of other coniferous species across different site and climate conditions. Although measurement procedures of resin ducts are much more time consuming than measuring ring widths, the results will provide new environmental information and an additional parameter useful in dendroclimatic reconstructions. New insights into the biological relationships can be achieved by investigating factors that control tree growth.

SUMMARY

A resin duct stem-analysis demonstrates the within-tree variability and the effects of cambium age on resin duct density. Particular years show extreme high resin duct densities, such as the dry year 1976, and these years show continuous bands throughout the stem. Summer temperature affects the formation of vertical resin ducts most. The periodicity of resin duct series are explored statistically using a set of samples extracted from 20 spruce trees. At a high frequency of about 3 years in the resin duct series a causal relationship can be seen with summer temperature. The current results should encourage researchers to investigate vertical resin ducts in tree rings.

ACKNOWLEDGEMENTS

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