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Original article

The growth of spruce (*Picea abies* (L) Karst) in the Krkonoše-(Giant) Mountains as indicated by ring width and wood density

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Summary — The spruce forests near the upper tree line in the Krkonoše Mountains (Czech Republic) are damaged by air pollution. Along an altitudinal transect, 141 spruces have been investigated to find out whether pollution has affected cambial activity indicated by changes in tree-ring width, maximum latewood density and a changing growth response to climate. Under severe pollution impact, a decline in both tree-ring width and maximum density was apparent. Correlation and multiple regression analyses of growth and climate point to a reduced length of the growth period in the last 2 decades. A possible relation to pollution impact is discussed.

Norway spruce / tree ring / latewood density / pollution / climate

Résumé — Croissance de l'épicéa commun (*Picea abies* (L) Karst) dans les monts Krkonoše : détermination par la mesure de la largeur des cernes et de la densité du bois. *Les peuplements d'épicéa commun (*Picea abies *L Karst) situés à proximité de la limite altitudinale des arbres dans les monts Krkonoše (République tchèque) sont affectés par la pollution atmosphérique. Un échantillon de 141 arbres a été sélectionné le long d'un gradient altitudinal pour examiner l'effet de la pollution sur l'activité cambiale par le biais des variations de la largeur des cernes de croissance, de la densité maximale du bois final ainsi que de la réponse de ces 2 paramètres au climat. Les niveaux élevés de pollution sont associés à une baisse de la largeur des cernes de croissance ainsi que de la densité maximale. Des analyses de corrélation et des régressions multiples indiquent une réduction de la période de croissance depuis quelques années. Le rôle possible de la pollution atmosphérique est discuté.*

épicéa / cerne annuel / densité du bois final / pollution / climat

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INTRODUCTION

The old growth spruce forests near the upper tree line in the Krkonoše Mountains in the Czech Republic are among the most damaged forests in Europe. Defoliation of the trees was recorded as early as 1979 (Vacek and Lepš, 1987). A preliminary dendroecological investigation in the upper Labe (Elbe) Valley revealed a growth depression since about 1970 and a subsequent recovery since the mid 1980s (Dobrý *et al*, 1992). The objective of the present study is to examine changes in tree-ring width and maximum latewood density as well as the changing response of the trees to climate, indicative of pollution-induced changes in the cambial activity of spruce.

MATERIALS AND METHODS

Altogether, 7 study sites were selected along an elevational transect from 1 000 to 1 300 m asl through the Labe Valley. On the southern slope, 90 spruces were sampled on 5 sites (sites 71–75); on the northern slope, 51 spruces on 2 sites (sites 77, 78) were selected. Tree age was between 70 and 220 years. Two cores per tree were taken for both the measurement of the annual increment and the wood density. The coring was done parallel to the slope to avoid compression wood.

The tree-ring widths were measured with an accuracy of 1/100 mm on a measuring device developed by Aniol (1987). The ring-width series were visually cross-dated, checked and corrected for missing and false rings, and statistically verified using the program COFECHA (Holmes *et al*, 1986). Those ring-width series, or parts of them, showing poor correlation with the so-called master chronology, were excluded from further analysis and the remaining series were averaged per tree. In order to differentiate exogenous disturbances from other growth influences, the series were detrended to eliminate the age trend and other long-term fluctuations (= standardization) using the program ARSTAN (Holmes *et al*, 1986). In the first step, the program fits a negative exponential function or regression line to each of the series and an index series was obtained. In a second step, a cubic spline (66 years stiffness) was fit to these index series. Remaining autocorrelation was removed by autoregressive modeling. The resulting series were aggregated by robust mean calculation into site-specific chronologies. A principal component analysis (PCA) of the total variation of all site chronologies was then computed to point out common patterns of the tree-ring width variation.

Maximum latewood density was measured by X-ray densitometry according to Schweingruber (1983) with an accuracy of 0.001 g/cm^3. The density series were dated and statistically treated as described earlier for the ring-width series, except that only a 1-step detrending was performed by fitting a cubic spline; autoregressive modeling was skipped because density series showed minor long-term fluctuations and extremely low autocorrelation. Like the ring-width series, the density series were averaged by robust mean calculation into site chronologies.

The climatic data used for calculating climate–growth relationships contained time series of mean temperature and the sum of precipitation per month from the Snezka Mountain (1 603 m asl), Harrachov (706 m) and Jakuszyce (871/910 m) stations. The data were checked for homogeneity and then aggregated into a regional climate chronology. Climate–growth relationships were computed by simple correlation and multiple regression analyses for the periods before and during severe air pollution impact from 1931 to 1960 and from 1961 to 1990, respectively. The climatic data were used as 1 variable and the chronologies of ring width and wood density indices as the other variables. Multicollinearity was avoided by using the principal components of the climatic data. These computations were conducted with the program RESPO (Lough, 1984; Holmes, 1994). Since response functions are sensitive to default parameters set in the program such as confidence level, number of eigenvectors and climatic parameters (Blasing *et al*, 1984), correlation analysis was also used as a means of confirming the resulting response function.

RESULTS AND DISCUSSION

The pattern of the ring-width series was very similar for all sample sites on the southern as well as the northern slope. The same was true for the latewood density series. However, there was no correspondence between these 2 parameters. Since the PCA did not reveal any grouping of the sites, slope chronologies for tree-ring width and latewood density were built. In table I, the statistics of both the ring width and the density time series are summarized.

Tree-ring width

The mean ring width of all trees investigated was 1.42 mm on the southern slope and 1.57 mm on the northern slope. Up to the 1960s, the trees on both exposures along the Labe River show the same growth level (fig 1); the annual increments decreased slowly from the pith outwards. After 1930, the years 1942, 1956, 1974 and 1980 are striking pointer years obviously caused by climatic influences: in 1942 and 1956 there were extreme frost events in January/February, and in 1974 and 1980 cold summers caused small increments. From about 1965 the southern-slope chronology diverged from the northern-slope chronology: whereas the spruces on the northern slope showed a slightly decreasing increment until the late 1970s and only a few years of growth depression from 1980, a long-lasting period of severe growth depression occurred in the southern-slope chronology. The trees started to recover as recently as the late 1980s. From 1974 on, an increasing number of missing and wedging rings were detected in many spruces on sites 71–75 (southern slope), but only in a few trees on sites 77 and 78 (northern slope). In all, 371 (= 1.2%) of the tree rings of the southern-slope spruces but only 54 (0.5%) of the northern-slope spruces were partly or totally missing. There was no apparent influence of tree age on this phenomenon. Old as well as younger trees showed disturbances in their cambial activity.

Maximum latewood density

Density series of the spruces on the northern and southern slopes showed a higher similarity than ring-width series (fig 2). According to correlation analysis, the strength of the common signal was higher in maximum density than in ring width. Whereas correlation coefficients for the ring widths reached 0.43 and 0.37 (chronologies of southern and northern slope, respectively), a coefficient of 0.63 was obtained for maximum density (table I). Until the early 1960s, maximum latewood density fluctuated around an average level of approximately 0.7 g/cm^3. In the recent period, density has been decreasing

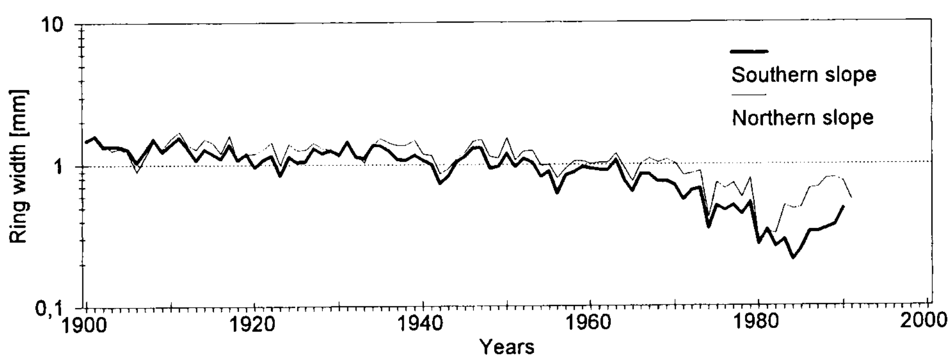

Fig 1. Ring-width chronologies of spruce in the upper Labe Valley.

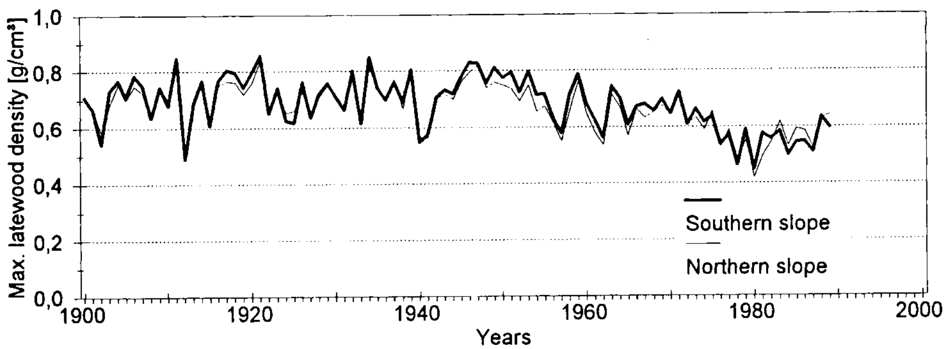

Fig 2. Maximum latewood density of spruce in the upper Labe Valley.

to below 0.5 g/cm^3. A comparable reduction was achieved only in 1912 when almost no latewood was formed (*eg,* Kyncl *et al,* 1990). The decline of maximum density can be caused by air-pollution impact. For example, Keller (1980) and Eckstein *et al* (1995) showed a decreasing amount of latewood production and a lower latewood density in spruce under the influence of SO_2 in fumigation chambers.

A comparison between tree-ring width and density chronologies showed no significant correlation. This phenomenon indicates that different factors affect cambial

Table I. Summary statistics of ring width and density series.

	Ring-width series		*Maximum density series*	
	Southern slope	*Northern slope*	*Southern slope*	*Northern slope*
Measurements				
Trees in chronology *(n)*	80	37	60	45
Length of chronology	1802–1990	1781–1991	1791–1989	1797–1990
Mean (mm) or (g/cm^3)	1.42	1.57	0.706	0.691
Mean sensitivity	0.18	0.20	0.14	0.13
Mean autocorrelation	0.90	0.85	0.33	0.44
Series intercorrelation	0.65	0.63	0.77	0.74
Detrending procedures				
1st detrending	regr line/neg exp fct		spline (stiffness 66 yrs)	
2nd detrending	spline (stiffness 66 yrs)		none	
Index chronology				
Mean sensitivity	0.14	0.17	0.09	0.11
Standard deviation	0.13	0.19	0.08	0.10
Correlation between trees	0.49	0.43	0.63	0.63
Signal/noise ratio	61.1	17.6	43.8	74.7
Variance in 1st eigenvector	50	45	64	66

activity, expressed by ring width, and cell differentiation expressed by density.

Climate–growth relationship

Temperature proved to be the most dominant growth-limiting factor for tree-ring width and density. This would seem to be reliable since the mean annual temperature in the Labe Valley does not exceed 4°C. Precipitation, however, reaches more than 1 300 mm per year and is therefore unlikely to be a limiting factor (Vacek, 1981). On the contrary, there is even a slight tendency for high amounts of rainfall to reduce tree growth (fig 3). The aspect of the sites had no effect on the trees' response to climate.

As was hypothesized from the comparison of the ring width and density chronologies, the climate–growth relationships of these parameters were different (figs 3, 4). In general, maximum latewood density reflected climatic influences more than ring width did. Eighty to 94% of the variance in the density chronologies and 61 to 77% in the ring-width chronologies could be explained by climate. Recently, climatic impact on ring width has been decreasing, but climatic impact on maximum density has been increasing.

From 1931 to 1960, ring width was affected by summer temperature (May to July). In the period from 1961 to 1990, the temperature of June alone was significant. Maximum latewood density was significantly influenced by temperature in early spring (April/May) and late summer (August) from 1931 to 1960. From 1961 to 1989, the period of influence was shortened to May and July.

To visually depict the climatic influence on both growth parameters, the respective index chronologies were plotted *versus* the record of the aggregated temperature data that had been shown to be significant (figs 5, 6). In the ring-width chronologies, the most distinct pointer years (1965, 1974, 1980) can be explained by cold summers; in 1940 and 1956, extreme frosts in January/February likely affected growth in the vegetation periods that followed. Pointer years in maximum density (1940, 1957, 1962, 1980) were caused by low temperature in May and/or in late summer. The significant relationship between precipitation in April/July and density was due to a few extreme data points or was caused indirectly by temperature (high temperature corresponded with low precipitation) and was not taken into further consideration.

It can be summarized that ring width is mainly correlated with temperature during the vegetation period, whereas latewood density mainly varies due to temperature at the very beginning and the very end of the vegetation period. This corresponds with results obtained for white spruce near the northern tree line (D'Arrigo *et al,* 1992) as well as for different conifers in the Alps and Scotland (Schweingruber *et al,* 1979). Cell-wall thickening in late summer seems to be connected with growth conditions in early spring, which affect the content of growth regulators, the development of the photosynthetic apparatus and the long-term supply of photosynthates. Under extreme climatic conditions near the upper tree line, the cessation of cambial activity and cell differentiation is not only related to the day length but, predominantly, to temperature. Short vegetation period and frost events that may occur in summer can cause the cessation of cambial activity and affect the duration of cell-wall thickening. This might explain the close relation of latewood density to temperature in July and August.

In the recent period, when trees have grown under the impact of severe pollution, the spruces in the upper Labe Valley showed an increasing occurrence of wedging and missing tree rings. This serious disturbance of cambial activity points to a lack of supply of assimilates and auxine. More-

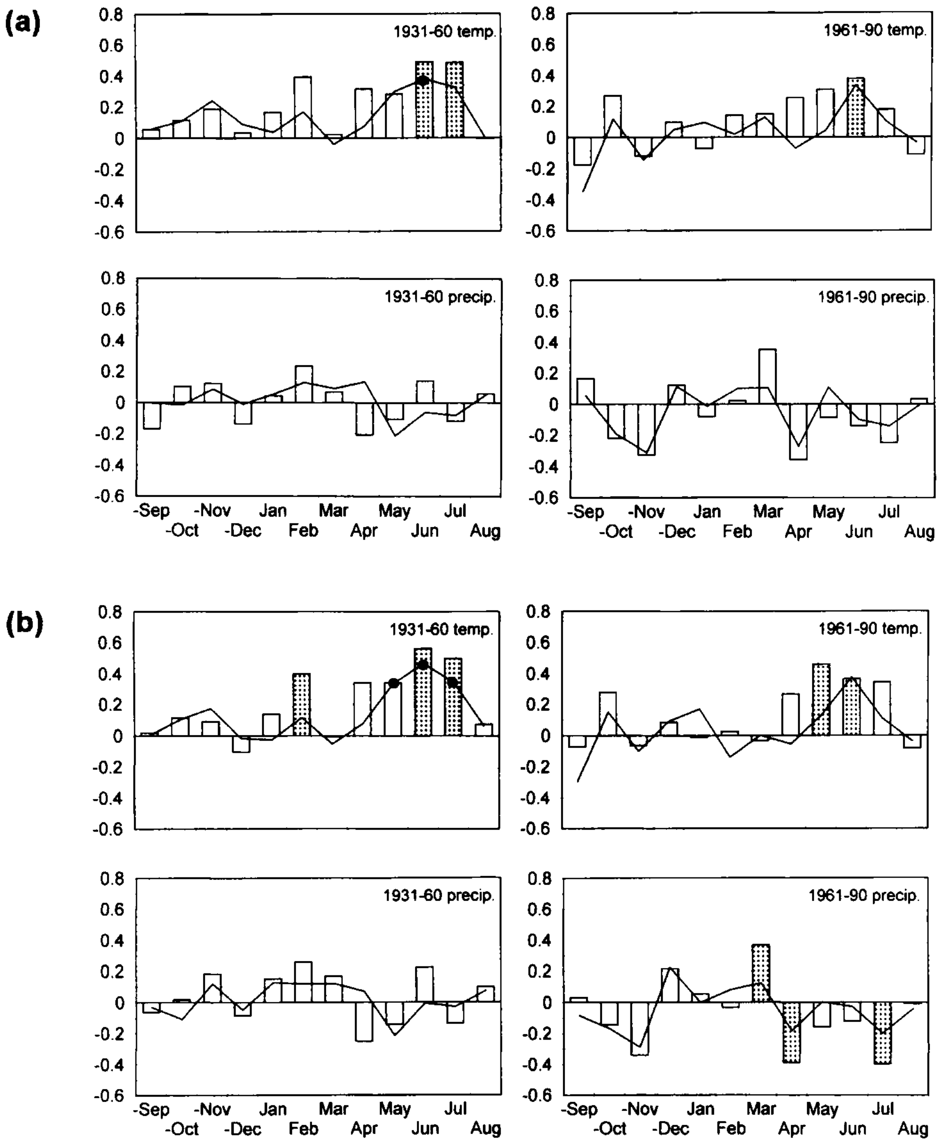

Fig 3. Response of the ring width to climate, obtained from simple correlation (bars) and multiple regression coefficients (lines). Significant coefficients are emphasized ($\alpha = 0.05$). (a) Southern slope, (b) northern slope.

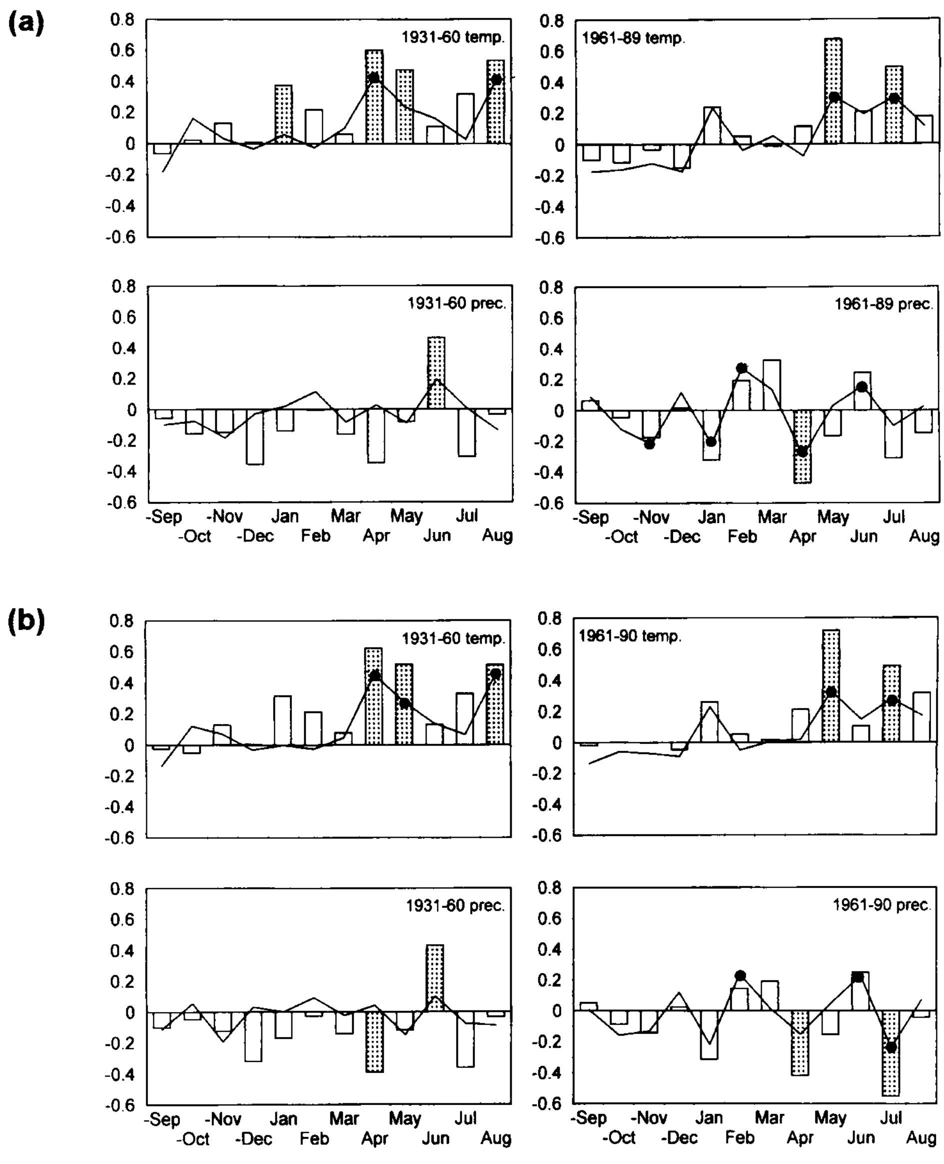

Fig 4. Response of the maximum density to climate, obtained from simple correlation (bars) and multiple regression coefficients (lines). Significant coefficients are emphasized ($\alpha = 0.05$). (a) Southern slope; (b) northern slope.

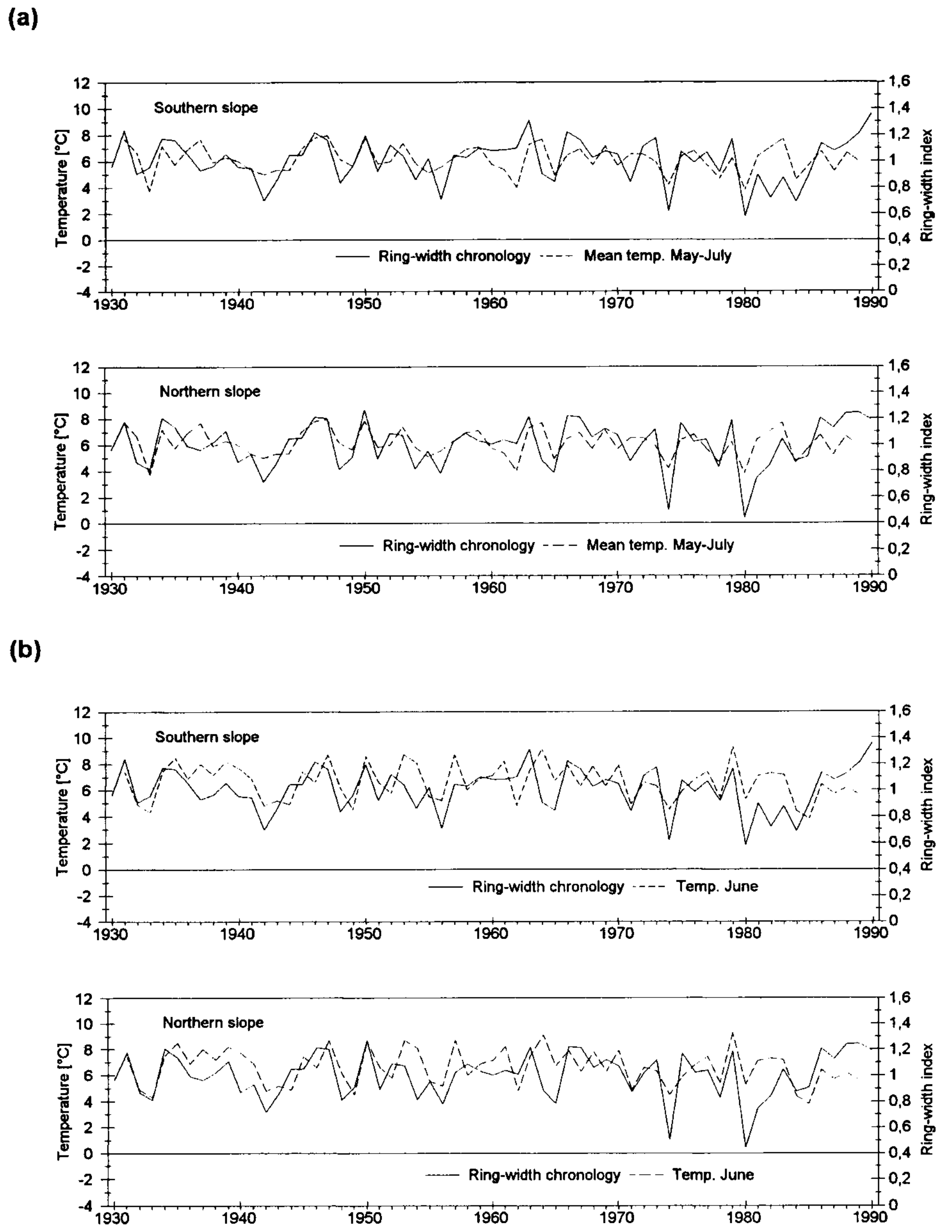

Fig 5. Ring-width chronologies compared to seasonalized climate: (a) mean temperature May–July, (b) temperature June.

(a)

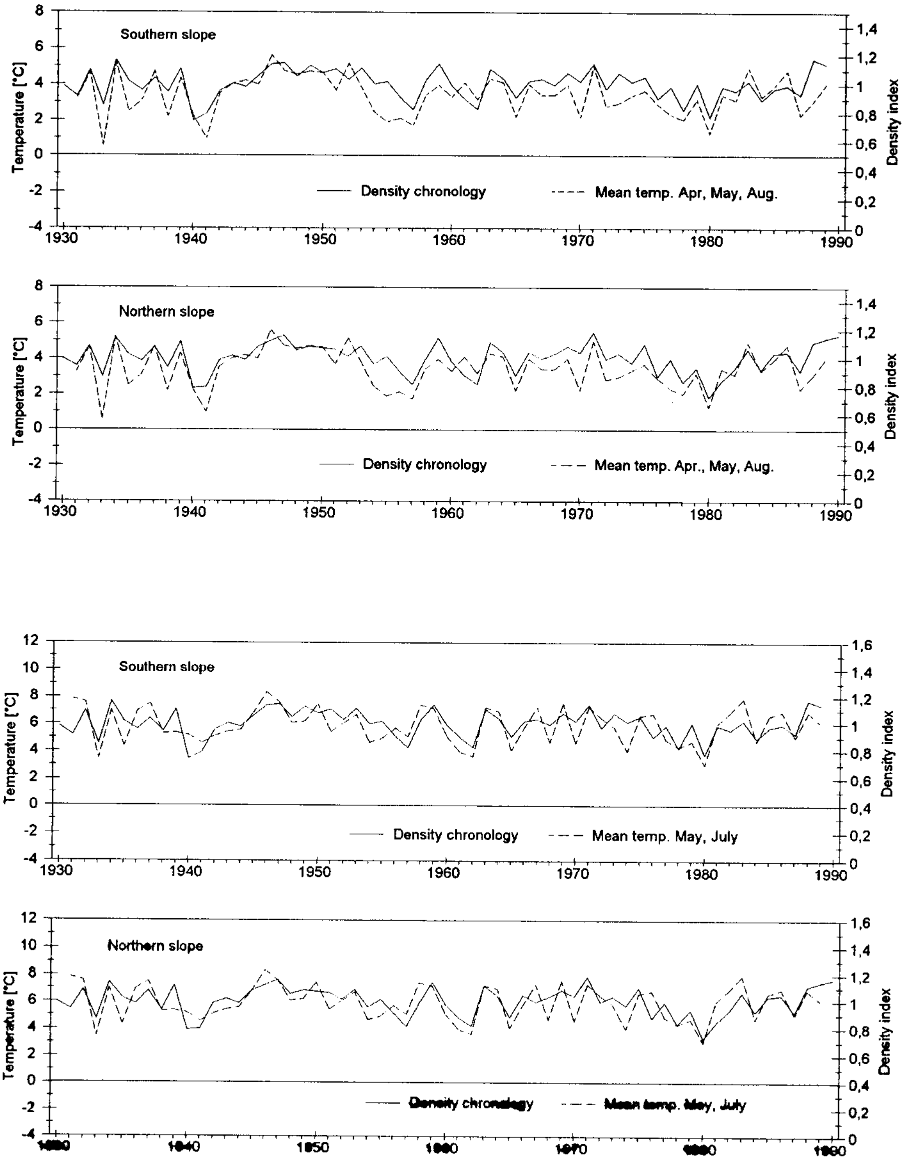

Fig 6. Maximum density chronologies compared to seasonalized climate: (a) mean temperature April, May, August; (b) mean temperature May, July.

over, the significant impact of temperature on both ring width and latewood density started later and ended earlier in the year. Since there are no data available on the periodicity of cambial activity of spruce in the upper Labe Valley, this result must be discussed further. This phenomenon implies that the period of cambial activity might have been shortened under pollution stress. Such a result has been observed by Götsche-Kühn (1988) in spruces showing severe needle loss: the duration of cambial activity was reduced by 60% relative to the duration observed in healthy trees. This can be explained by pollution-caused inhibition of photosynthesis and synthesis of hormonal growth regulators which are dependent on the development of buds and shoots (Kozlowski, 1986); this may also hold true in the Labe Valley.

An additional effect of climate is also conceivable. It has to be considered that the mean summer temperature has decreased. The mean July and August temperatures during the period from 1961 to 1989 recorded at Snezka Mountain were 8.0/8.0°C compared to 8.7/8.5°C for the 30 years before. Under the growth conditions along the upper tree line, this may have contributed to shorten the vegetation period. However, mean spring temperature did not change, thus the later initiation of cambial activity cannot be explained by climate.

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