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Oak decline in southern Moravia: the association between climate change and early and late wood formation in oaks

Odumírání dubů na jižní Moravě v důsledku vlivu klimatických změn na tvorbu jarního a letního dřeva

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Pedunculate (*Quercus robur*) and sessile (*Quercus petraea*) oak, dominant species in European hardwood forests, are declining in many regions throughout Europe and extreme climatic events (summer drought, winter frost) are considered to be key factors contributing to this decline via a negative effect on wood formation. An extensive sampling of scattered oak trees within a landscape of small groves and flower meadows in the White Carpathians, a hilly chain in the warm south-eastern part of the Czech Republic, was undertaken in order to determine the association between growth in diameter and climate over the last 100 years. The association with climate was evaluated by comparing late wood, early wood and total ring widths with monthly climatic data over the period 1900–2006, using a combination of response function and pointer year analyses. The two approaches clearly showed that late wood growth of oak trees, growing on deep calcium-rich soils, which dry out in summer, is mainly associated with rainfall in May–June, while early wood growth is associated with previous autumn and winter temperatures. Extreme growth years coincided with an abnormally wet or dry May–June periods, which are often associated with cool or hot Junes. Deficient water balances resulting from low rainfall and high temperatures during the summer period are negatively associated with late wood formation and hence total annual growth increment. The results provide support for a crucial role of climate change (decline in rainfall and increase in summer temperatures over the last three decades) among other external factors in the high number of oaks dying prematurely in the White Carpathian wooded grasslands. Prolonged periods of unfavourable climatic conditions cause attenuated trees to become prone to fungal attack and mistletoe hemiparasites, which predispose the oaks to damage or death, especially solitary pedunculate oaks.

Keywords: aridity index, climate-growth relationship, moving response function, pointer years, potential evapotranspiration, *Quercus petraea*, *Quercus robur*, severe drought, tree-ring analysis

Introduction

In many regions throughout Europe pedunculate (*Quercus robur* L.) and sessile (*Quercus petraea* L.) oak, dominant species of European hardwood forests (Dimopoulos et al. 2005), are dying (Siwecki & Ufnalski 1998, Helama et al. 2009). The virulent contagion, called oak decline, slowly kills the plant from the top down. It is predicted that global warming will result in the disease spreading even more quickly in the future (Drobyshev et al. 2007). This, and other reasons have stimulated research on these species, both on a national and a European level (Thomas et al. 2002), and factors affecting their diameter growth are being intensively studied using dendrochronological tree-ring analysis (Lebourgeois et al. 2004).

Historical records and dendrochronological measurements indicate that oak decline has occurred repeatedly in Europe over the past three centuries (Thomas et al. 2002). The first indication of oak decline is the progressive dieback of leaves beginning at the tips of the branches in one-third to one-half of the upper canopy. Other symptoms may include chlorotic, stunted or sparse foliage; epicormic shoots on the main trunk and larger branches; cracks in the bark at the bases of trees; patchy discolouration of sapwood (seen in cross-sections); premature leaf senescence and browning with the leaves remaining on the trees (Wargo et al. 1983, Butin 1995). Often, there is a decrease in the size of the annual rings before the trees show symptoms of disease.

Symptoms have been attributed to insect pests, fungal attack, mistletoe hemiparasites, secondary defoliation caused by powdery mildew, or mineral deficiency (Jung et al. 1996, Gibbs & Greig 1997). In addition, extreme climatic events (summer drought, winter frost) are thought to be important factors in oak decline (Dwyer et al. 1995, Siwecki & Ufnalski 1998). In the context of rising temperatures and the potential effects of exceptional heat waves, concern is being expressed about the growth and survival of oak.

This paper aims to explore the association between climate and the yearly variation in radial growth of pedunculate and sessile oaks in the White Carpathians, a hilly chain in the warm south-eastern part of the Czech Republic. The area is renowned for its high plant and insect diversity associated with savanna-like grasslands (with scattered *Quercus* spp. trees), traditionally managed by mowing once a year followed by autumn grazing (Klimeš 1995). Although many hay meadows in the White Carpathians were lost during the land consolidation schemes in the 1970s and 1980s, over 2000 hectares were preserved in a dense network of reserves. The reserves consist of flower rich meadows, interspersed with scattered *Quercus* trees and small woods, in which there has been a high level of tree mortality over the last three decades, which cannot be explained solely by factors associated with senescence (Jongepierová 2008). Extreme climatic events such as summer drought (together with higher rates of mistletoe infection) are thought to be responsible for the recent decline in the abundance of oaks.

In this paper, this idea is tested by analyzing wood formation in relation to climatic variables. The most important climatic factors associated with tree growth were identified (i) by establishing the mean relationships between tree ring residual chronology and climate through bootstrap moving correlation and response-function analysis (Biondi & Waikul 2004), and (ii) by distinguishing "pointer years", which correspond to abrupt changes in growth pattern and reveal the response of trees in terms of growth to extreme climatic events (Schweingruber 1996). Since oaks are ring porous species with an abrupt transition between early and late wood, both parameters are easy to measure and can be used to obtain subseasonal climatic information (Zhang 1997, Lebourgeois et al. 2004). The effect of climate on different components of radial growth was assessed in order to determine the climatic factors that are associated with wood formation at different times of a year.

Study area

The research was carried out in the National Nature Reserve (NNR) of Čertoryje, the White Carpathians, a hilly (maximum alt. 970 m) chain formed of base-rich flysch sediments, adjoining the Czech/Slovak border and a landscape protected area of 748 km^2. The

Fig. 1. – The wooded grasslands of the National Nature Reserve of Čertoryje, the White Carpathians, Czech Republic, with scattered oaks (upper) and small groves (bottom), where the tree-ring study was done.

landscape consists of villages in narrow valleys, steep slopes covered by deciduous woodlands, and grasslands on shallow slopes and plateaus. Owing to the remoteness of the area, the region was the last in the Czech Republic to be affected by the communist-era land consolidation, and small private farmers retained their land until the early 1980s. The traditional land use created and maintained mosaics of meadows, pastures, small fields, orchards and woods. Grasslands cover 20% of the landscape protected area, mainly in the form of savannah-like 'Carpathian meadows' (Fig. 1). They are famed for their exceptional floral richness (Klimeš 1995, 1999) and diversity of *Lepidoptera* (Králíček & Gottwald 1984). Mean annual temperatures are 8.8 °C, 8.5 °C and 9.1 °C, and mean annual rainfall 699 mm, 727 mm and 674 mm for the periods 1900–2006, 1900–1950 and 1951–2006, respectively.

Methods

Sample collection

The area sampled was situated in grassland with scattered *Quercus* spp. trees, at an altitude of 430–440 m a.s.l., on a west-facing slope of NNR Čertoryje with an incline of about 5°. Soils are relatively deep and calcium-rich, drying out in summer. Cores were obtained from 107 randomly selectecd trees (66 from *Q. robur*: 51 solitary, 15 closed-canopy, and 41 from *Q. petraea*: 30 solitary, 11 closed-canopy) by boring their trunks 1.3 m above ground level using 200–600 mm long Swedish increment borers (Mora, Sweden). The majority of the trees selected did not have hollow trunks. Cores were sanded and inspected for reaction wood and other aberrant properties at the laboratory of the Institute of Botany AS CR in Třeboň using standard dendrochronological procedures (Cook & Kairiukstis 1990). Tree-rings were counted from pith to bark and their widths measured to the nearest 0.01 mm with the aid of a microscope interfaced with a computer. For approximately 15% of the cores, which lacked pith, the number of missing rings was estimated from the diameter of the innermost tree-ring and the average width of the five following rings.

PAST4 was used (www.sciem.com) for crossdating and quality control, and ARSTAN (Cook 1985) for determining the chronology using a conservative detrending of negative exponential and straight line curve fits (Cook & Kairiukstis 1990). Then any remaining autocorrelation was removed by autoregressive modelling, which removes biological trends and enhances climatic signals. From the three chronologies (standard, residual, Arstan), residual chronologies with the strongest common high-frequency variation were used. The residual series (individual samples) were averaged to produce a set of annual growth indices for early wood (EW), late wood (LW) and total ring (TR) widths. The final chronologies for *Q. petraea* included 31 cores for the period 1893–2006 with a mean series intercorrelation of 0.39, 0.41 and 0.51 and an average mean sensitivity of 0.13, 0.22 and 0.19 for EW, LW and TR, respectively. The final chronologies for *Q. robur* included 42 cores for the period 1898–2006 with a mean series intercorrelation of 0.58, 0.56 and 0.48, and an average mean sensitivity of 0.14, 0.21 and 0.17 for EW, LW and TR, respectively. The two regional chronologies are similar to the oak chronologies from other localities in Moravia (T. Kyncl, unpublished data) such as Zouválka (r = 0.54 and 0.39 for *Q. petraea* and *Q. robur* total ring widths, respectively), and Ždánický les (r = 0.31 and 0.33 for *Q. petraea* and *Q. robur* total ring widths, respectively).

Data analysis

Relationships between ring-width chronologies and climate variables were studied using bootstrap moving correlation and response-function analysis in the DENDROCLIM program (Biondi & Waikul 2004). Monthly mean temperature and monthly total rainfall recorded at meteorological stations in Velká nad Veličkou (rainfall records for the period 1961–2007, 250 m a.s.l., 7.5 km E from the NNR Čertoryje), Strážnice (temperature records for the period 1941–2007, 200 m a.s.l, 10 km W from the NNR Čertoryje) and Vienna (temperature record for the period 1775–1995, rainfall record for the period 1845–1993, 140 km SW) were compiled. Furthermore, there is monthly total rainfall data available for the period 1898–1996 for southern Moravia, which were collected for a fir tree-ring study using March-July rainfall (Brázdil et al. 2002). The DPL-HOM program was used to determine the homogeneity of the climatic data (Holmes 1994).

As climatic data from Velká nad Veličkou and Strážnice were highly correlated with climatic series from Vienna and southern Moravia (mean r^2 of 0.87 for linear regressions between Strážnice and Vienna temperatures for the period 1941–1995, and mean r^2 of 0.64 for linear regressions between Velká nad Veličkou and southern Moravia rainfall for the period 1961–1996) long-term site temperature and rainfall series were developed from available climatic records using linear regression. The radial growth was further related to differences in rainfall and potential evapotranspiration (PET), calculated using the empirical equation of Jensen & Haise (1963) and daily values for solar radiation and temperature:

$$PET = [Rs / 2450 \cdot ((0.025 \cdot Ta) + 0.08)]$$

where: PET = mean daily potential evapotranspiration (mm/day), Rs = daily total solar radiation (kJ/m^2/day), Ta = mean daily air temperature (°C). Solar radiation data were obtained from satellite (http://www.satel-light.com). Indices of rainfall effectiveness (rainfall compared with PET, P-PET) and the aridity index as ratio of rainfall and PET (UNEP 1992) were calculated.

Finally, explanatory climate variables spanned a 15-month window, from July of the previous year to October of the current growth year. As tree-ring and climatic series go back to the19th century, moving correlation and response functions were calculated (Biondi 1997) with the residual chronologies for early wood, late wood and total ring width indices using a 60-year window shifted in time. By doing this the temporal stability of climatic signals identified for those bioclimatic units was investigated (Di Filippo et al. 2007). The response function analysis is based on stepwise multiple regression, where climatic variables are used after their transformation into principal components. The significance is tested using bootstrap techniques (Guiot 1991).

The pointer years were distinguished in each early wood, late wood and total ring chronology as abrupt changes in growth pattern (a strong relative increase or decrease, > 10%, found in at least 70% of the crossdated trees at a site) (Schweingruber 1996). The pointer years analysis provides information on an individual year basis and supplement the calculation of correlation and response functions, which provide information about the dominant mode of the linear response between tree-ring and the common mesoclimatic variables over many years (Fritts 1976).

Results

Climate

Long-term meteorological records show positive trends in mean spring, fall and winter temperatures since the 1850s with warming more pronounced in the spring (Fig. 2). The records also show a substantial increase in summer temperature since mid 1980s. The 1990s were the warmest interval in the last 150 years. These records also reveal there was less rainfall in the second half of 20th century. In particular, there was a decrease in spring and summer rainfall in the 1970s. The 1970s–1990s was the longest period of dry years over the last 150 years, particularly so during the summer months.

Age and characteristics of the annual rings of the cored trees

The age of *Q. robur* trees ranged from 16 to 132 years in 2006, with a mean of 70 years. The age of *Q. petraea* trees ranged from 25 to 130 years, with a mean of 65 years. The average widths of the early wood, late wood and complete rings was 1.01, 1.51 and

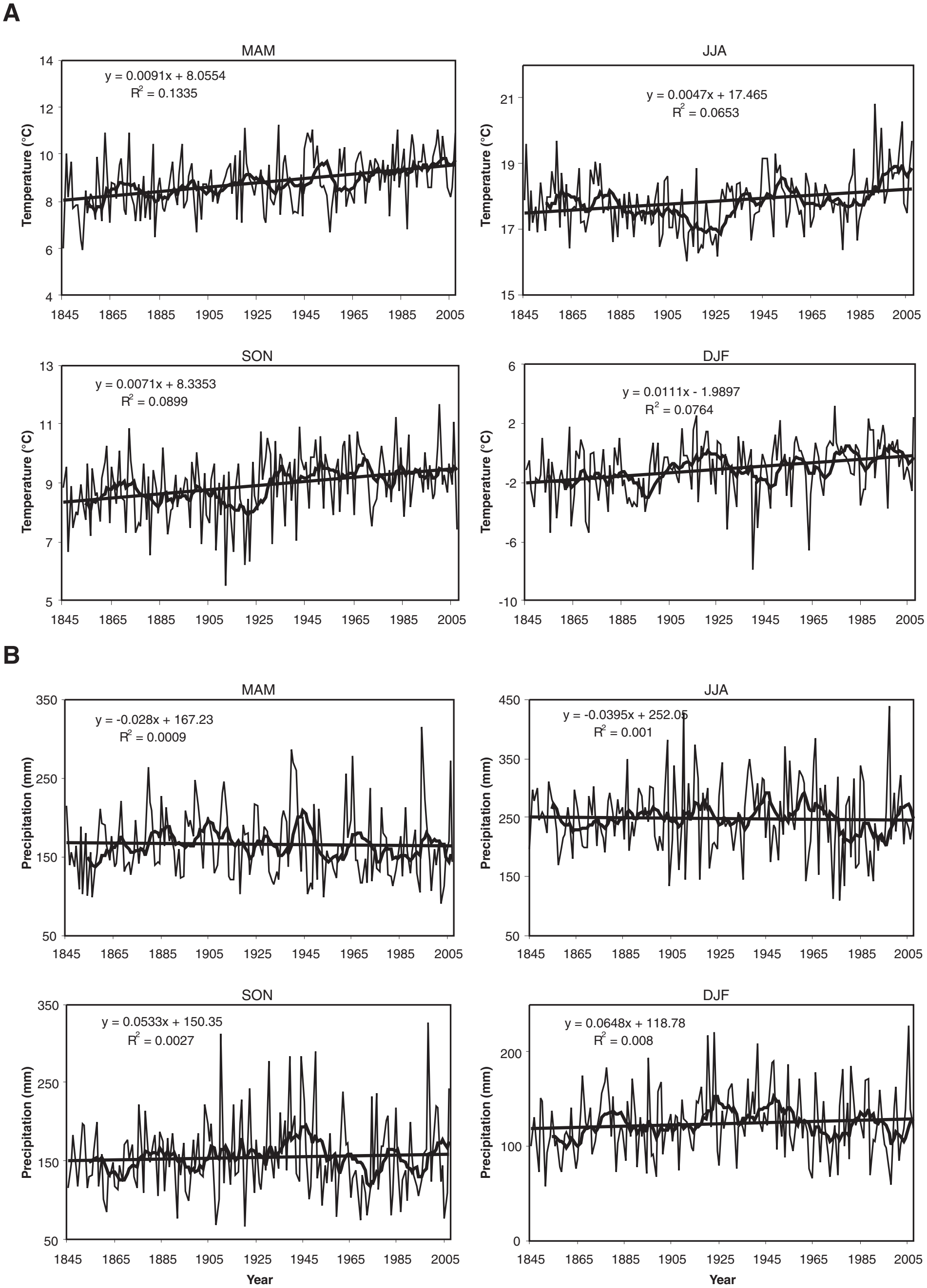

Fig. 2. – The average tmperature (A) and rainfall (B) recorded in the study area for the spring (MAM), summer (JJA), autumn (SON) and winter (DJF) periods, with smoothed values (10 year running mean) and fitted linear regression.

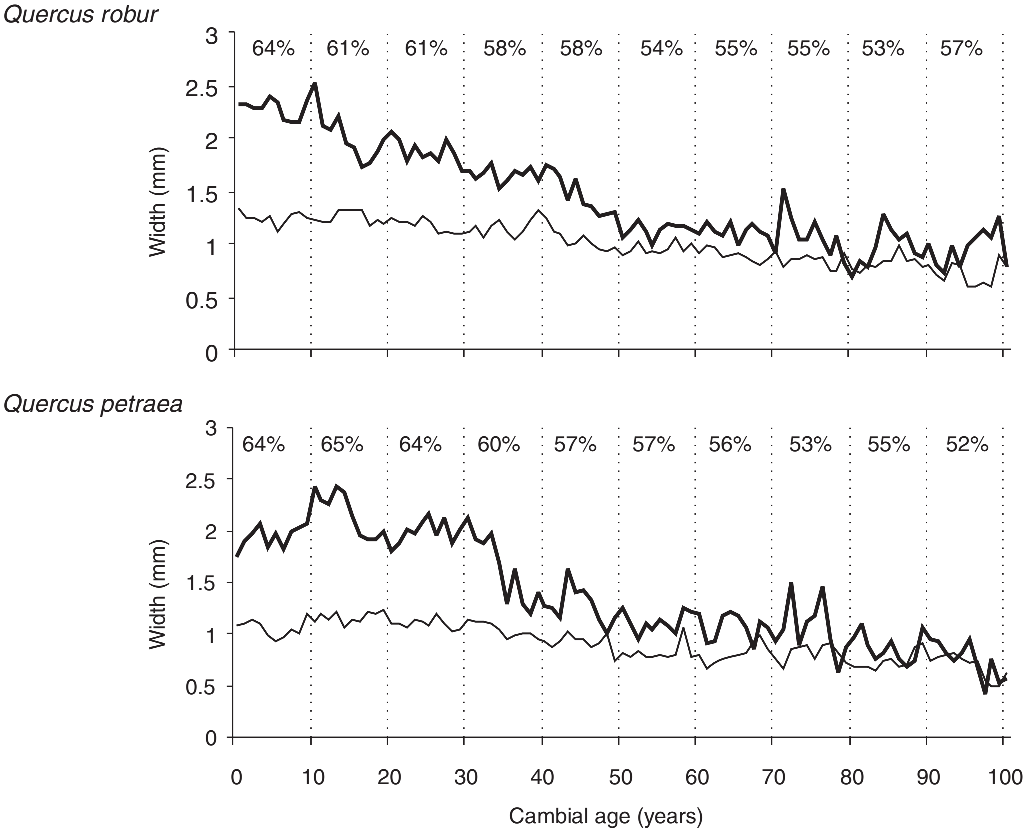

Fig. 3. – Early wood (thin line) and late wood width (thick line) in relation to cambial age. For each ring, the cambial age corresponds to the age of the tree when the ring was formed. Percentages indicate mean late wood/total ring width ratio for each decade.

2.52 mm for *Q. robur* and 0.88, 1.31 and 2.21 mm for *Q. petraea*, respectively. Proportion of late wood in *Q. robur* ranged from 72 to 47% of each ring width according to cambial age, and from 67 to 28% in *Q. petraea* (Fig. 3) and there was a strong positive correlation between complete ring width and late wood width (r = 0.98 for *Q. robur* and 0.99 for *Q. petraea*). The late wood width mainly determined tree-ring width, while the early wood width was more constant from year to year.

Correlation and response analysis

The values of the moving correlation function of the width of oak tree-rings with rainfall and air temperature in the 15 months preceding September of the year of growth are shown in Fig. 4. Positive values of the correlation coefficients indicate that higher values of the climatic characteristic in a given period are associated with a positive effect on the growth of the trees, and vice versa. Each cell (last year of the time interval) represents an association with climate in a particular month over a period of 60-years. The results of simple cor-

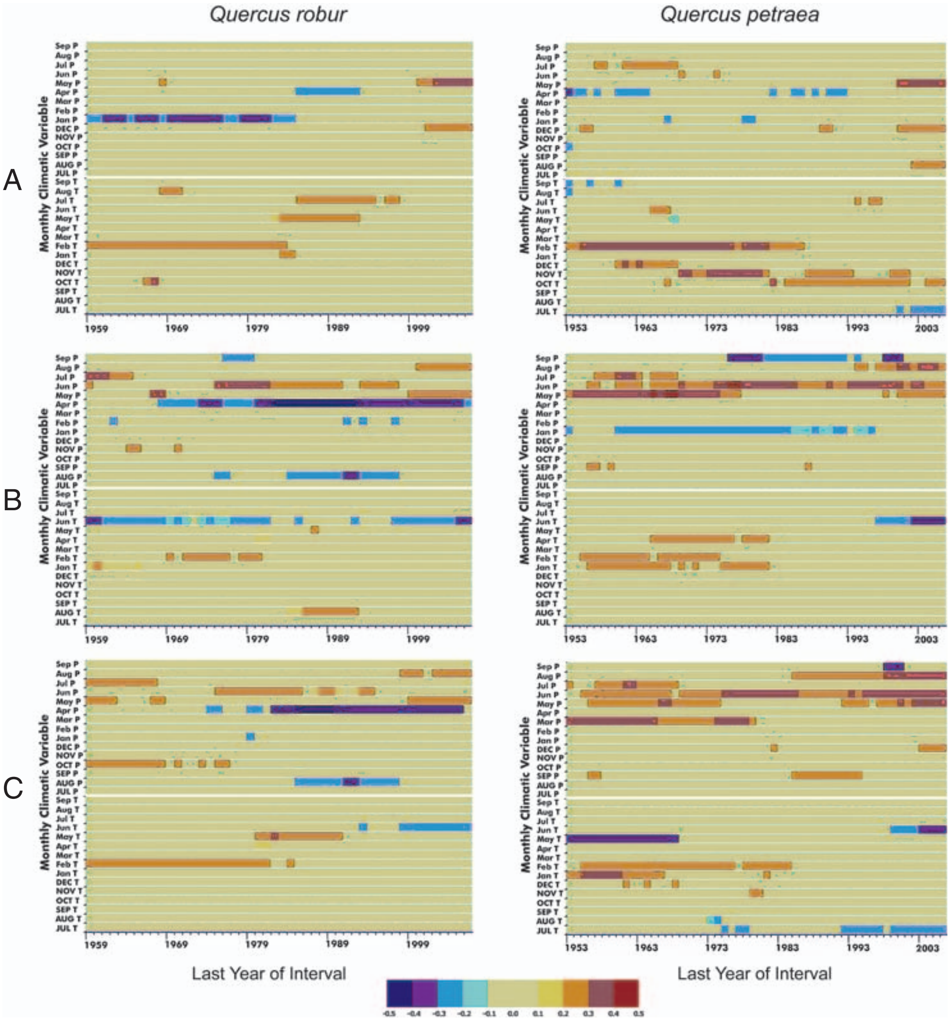

Fig. 4. – Moving correlation function for early wood (A), late wood (B) and total ring (C) width. Each cell (last year of time interval) represents a reaction to climate in a particular month in a 60-year time period from 1899-2006 for *Quercus robur* and from 1893-2006 for *Quercus petraea*.

relations and response function analyses were consistent and indicated that late wood chronologies are more closely associated with rainfall (hydric balance) in the current growing season and early wood chronologies with air temperature in the previous autumn and winter (Fig. 4). The response function coefficients were similar but slightly lower than those of the correlation analysis (results not shown).

A warm autumn the previous year and warm and less snowy winters are positively associated with early wood formation. An increase in early wood growth was associated with a warm October and November the previous year, and a warm January and February (with the strength of the correlation decreasing from 1980s onwards) and a decrease with snow/rain in January and April (*Q. robur*). The positive association of early wood formation

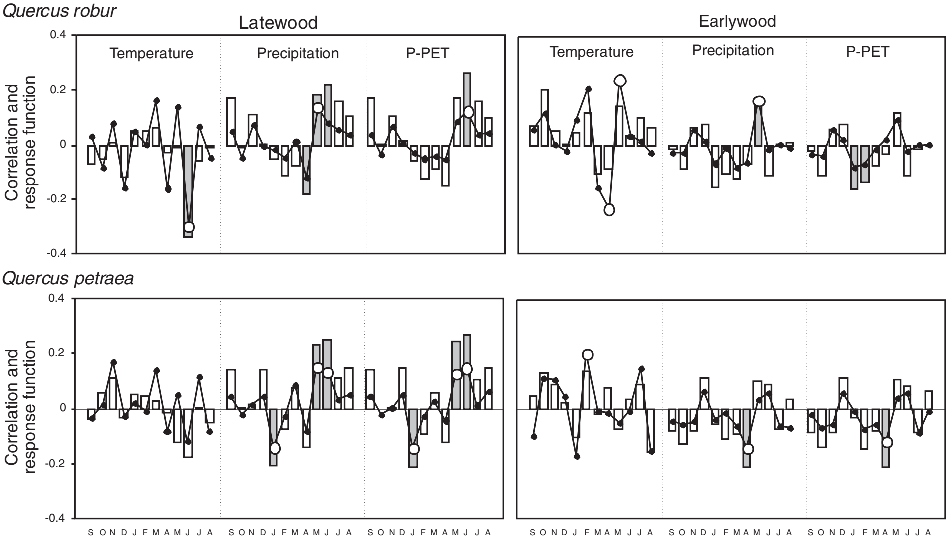

Fig. 5. – Correlation (columns) and response function (dots on line) of the indices of early wood and late wood widths to three climatic variables (P-PET = precipitation minus potential evapotranspiration) calculated for a 12 month period (September of the previous year to August of the current year) for the years 1899–2006 for *Quercus robur* and 1893–2006 for *Q. petraea*. Months with significant correlations are indicated by shaded columns, empty bullets indicate months with significant responses.

with autumn temperatures the previous year was more pronounced in *Q. petraea,* with the strength of the association increasing in the last three decades. The association with temperature the previous autumn in *Q. petraea* shifted from November to October in the late 1970s.

Late wood production in both species is associated positively with rainfall in May–June, with the highest correlation with June rainfall. While the positive association with rainfall in *Q. petraea* shifted from May to June in the 1980s, the opposite shift occurred in *Q. robur* in the late 1990s (Fig. 4). For both late wood and total ring width, a positive association with rainfall in the growing season was often associated with a negative association with temperature in the current growing season (May, June), indicating the inter-relation between mean monthly temperatures and rainfall. The late wood growth in *Quercus robur* was negatively associated with high April rainfall and June temperatures, but not in *Q. petraea* (Figs 4, 5). Total ring width in *Q. robur* was also negatively associated with April rainfall, with the strength of the association increasing in the 1980s–1990s. Total ring width in both species showed a positive association with high rainfall in late spring and summer.

Pointer years

For the period 1899–2006 (108 years), a total of 46 years for *Q. petraea* and 38 years for *Q. robur* are defined as pointer years, either for total ring, early wood or late wood widths (Table 1). A total of 23 and 20 corresponded to high-growth years and 23 and 20 to low-growth years in *Q. petraea* and *Q. robur*, respectively. In both species the number of pointer years was higher for late wood (32 and 29 years in *Q. petraea* and *Q. robur*) than for early wood (10 and 11 years). There was a close association between total ring and late

Table 1. – Calendar years characterized by a strong relative increase (positive pointer years) or decrease (negative pointer years) in radial growth of each ring component in *Quercus petraea* and *Q. robur*. TR – total ring; EW – early wood; LW – late wood. The years are those in which a strong relative increase or decrease (> 10%) is recorded in at least 70% of the crossdated trees. AI is the aridity index, which is the ratio of rainfall in May–June to potential evapotranspiration in these months.

Quercus petraea										*Quercus robur*									
Positive pointer years					Negative pointer years					Positive pointer years					Negative pointer years				
Year	TR	EW	LW	AI	Year	TR	EW	LW	AI	Year	TR	EW	LW	AI	Year	TR	EW	LW	AI
2001	63		121	0.89	2003			–23	0.65	2001	53	44	67	0.89	1993	–23		–29	0.46
1999	20			1.07	1998	–20		–21	0.53	1994	22		42	1.19	1992	–19		–26	1.04
1994	36	27		1.19	1993	–18		–21	0.46	1991	24		37	1.05	1983	–15			0.61
1982	58		83	1.01	1992			–24	0.58	1982	63	44	82	1.01	1976	–18		–27	0.58
1980	45			0.72	1983	–19		–30	0.61	1981	42		88	0.61	1973	–23		–30	0.32
1975	46		104	1.16	1979	–24		–40	0.72	1969	39		51	0.99	1956	–32		–37	0.77
1969	26	20		0.99	1976	–27		–45	0.58	1959	30		63	1.08	1947	–29		–34	0.46
1961	23	32		1.23	1970	–14	–8	–19	0.65	1951	29		36	1.31	1935	–31			0.90
1960	31			0.99	1958			–12	0.80	1949	35			1.15	1928	–15			0.66
1951	39		54	1.31	1954	–23		–26	0.89	1945	34		43	0.76	1927	–17		–14	0.70
1949	22		46	1.15	1947	–27		–28	0.46	1936	73			1.18	1922	–29		–26	0.38
1944	28			1.41	1945			–11	0.76	1932	32			0.64	1915	–23	–18	–9	0.93
1936	34		105	1.18	1934		–6		0.58	1925	40	92	18	1.01	1912	–41		–49	1.25
1935	37	47	41	0.90	1933	–32		–43	0.94	1924	94			1.05	1909		–44		1.37
1931	35		57	0.43	1930			–8	0.58	1919	60	58	60	1.10	1908	–35		–55	0.40
1925	38		41	1.01	1928	–14			0.66	1908		56		0.40	1904	–23		–32	0.59
1924	60			1.05	1922	–47	–34	–52	0.38	1907	38	30	40	0.53	1901	–31	–20	–34	0.62
1916			4	0.98	1915	–14		–23	0.93	1906	101		142	1.19	1900	–33	–14	–37	0.89
1914		20		0.85	1913	–19		–18	0.66	1903	18		23	1.28	1899	–21	–21	–21	0.95
1909	3			1.04	1908			–27	0.40										
1907			24	0.71	1904			–39	0.59										
1906	26			1.19	1901	–39	–47	–18	0.62										
1900	28	43	15	0.89	1899	–16			0.95										
Total/ Mean	20	6	12	1.02		15	4	20	0.65	Total/ Mean	18	6	14	0.97		18	5	15	0.73

wood width, although in some years late wood varied independently. Among the 35 pointer years defined in terms of total ring width for *Q. petraea*, 10 are not pointer years for late wood width. For *Q. robur*, 7 of the 36 pointer years for total ring width were not pointer years for late wood width. The positive years 1935, 1900 and the negative years 1970, 1922 and 1901 were the same for each ring component in *Q. petraea*. The positive years 2001, 1982, 1925, 1919 and 1907 and the negative years 1915, 1901, 1900 and 1899 were the same for each ring component in *Q. robur*. No period lacked signature years for *Q. petraea*, with at least three pointer years in each decade (3 to 7; mean: 4/10 years). There was a close association between late wood pointer years and extreme spring precipitation (Figs 6, 7). For *Q. petraea*, 16 of the 20 low-growth years and for *Q. robur,* 11 of the 15 low-growth years, are associated with spring droughts (average for May and June precipitation is 75 and 94 mm, respectively, for the 1899–2006 period), in particular in 1993 (May 46 mm), 1992 (May 18 mm), 1976 (June 35 mm), 1973 (May 25 mm and June 40 mm), 1970 (May 27 mm), 1956 (May 40 mm), 1922 (May 30 mm), 1915 (May 18 mm), 1908 (June 19 mm) and 1904 (June 46 mm) (Fig. 7). In contrast, the positive pointer years are often associated with rainy summers. This was particularly so for the positive years

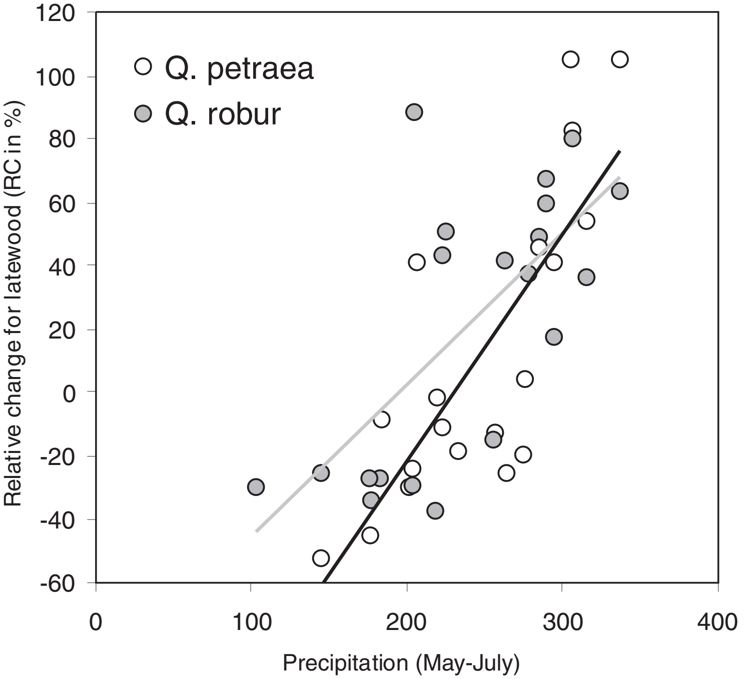

Fig. 6. – Correlation between the relative change in growth of late wood in pointer years calculated for the period 1921–2001 and rainfall sums for May–July (in mm). *Quercus robur*: $y = 0.48x – 93.65$, $r^2 = 0.47$; *Q. petraea*: $y = 0.71x – 164.15$, $r^2 = 0.62$.

2001, 1982, 1975, 1951, 1936, 1926, 1910, 1906 and 1903, which had wet (MJJ precipitation > 300 mm, average for the period 1899–2006 is 252 mm) and relatively cool summers (–1.5 °C below normal value). For *Q. robur* rainfall in April seemed also to be associated with late wood signature years. The positive pointer years are often associated with below average rainfall in April (early onset of growing season during dry and warm April), followed by a "humid" summer as in 1982 (April P = 11 mm, average for the 1899–2006 is 54 mm), 1975 (35 mm) and 1969 (12 mm). A similar pattern is recorded for total ring width.

Low rainfall in January and high temperatures in February are also associated with signature years. This is particularly true for the negative years 1901 (February T = –4.8°C, average for the 1899–2006 is –0.3 °C), 1909 (–3.6 °C) and 1929 (–11.3 °C), but also 1947 (–5.9 °C) and 1956 (–10.9 °C), which were characterized by cold winters. The positive pointer years for *Q. robur* are often associated with high February temperatures (1–2 °C above normal value), as in 2001 (1.5 °C), 1925 (3.11 °C) and 1908 (0.9 °C), and below-normal January rainfall (< 20 mm, the long-term mean is 37 mm).

Discussion

Scattered oak trees and small groves are important components of White Carpathians flower meadows (Jongepierová 2008). Their present-day savanna-like or parkland appearance is, however, not always seen in aerial photographs taken in the first half of the 20th century. The range of ages of the trees in the NNR Čertoryje suggests that individuals

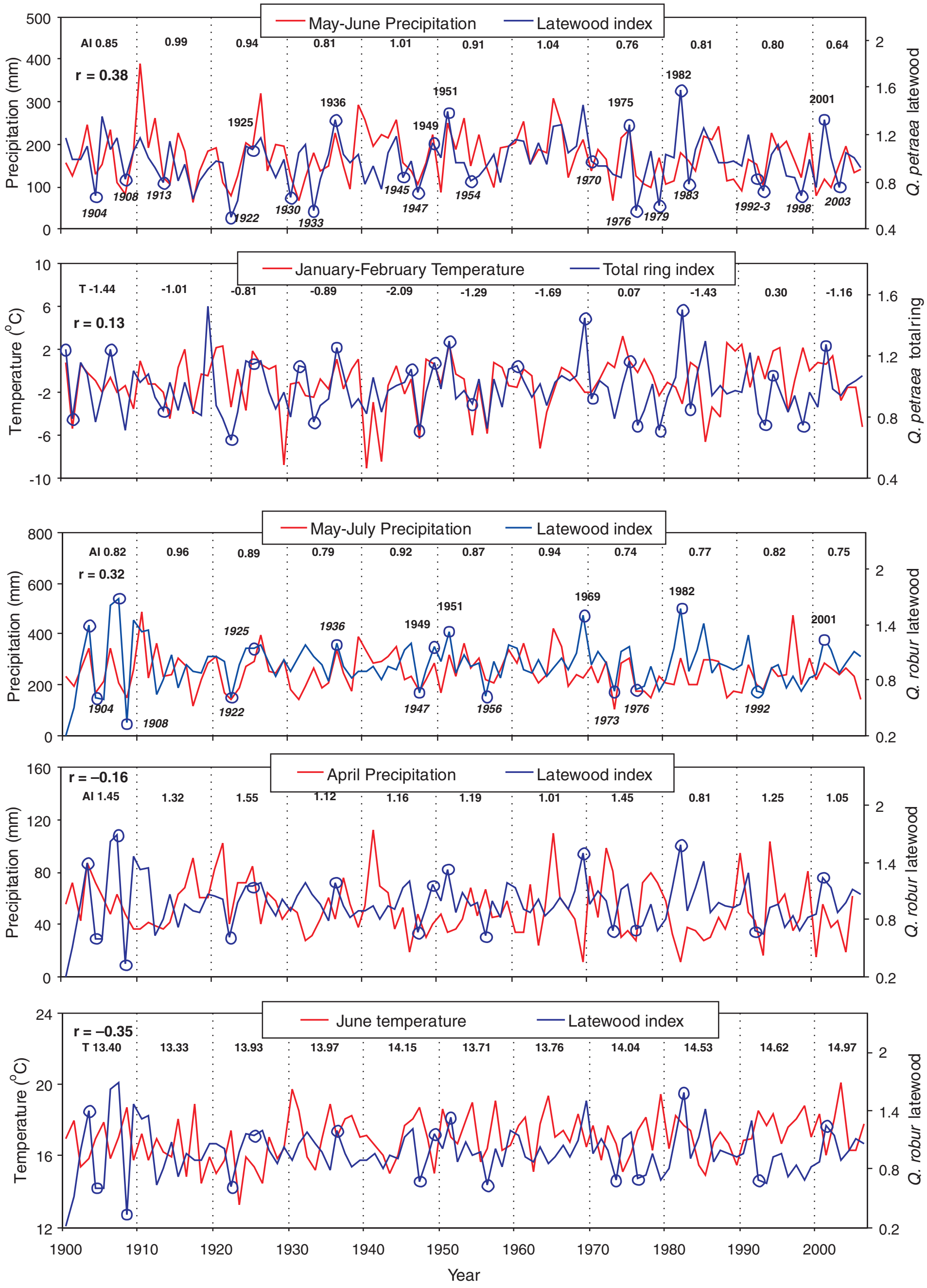

Fig. 7. – Comparison of the late wood and total ring indices for *Quercus petraea* and *Q. robur* with rainfall and temperature. The open symbols correspond to the pointer years. Decadal means of the aridity index (AI) and mean monthly temperatures (T) are shown at the top of the graph. The correlation coefficients for the climatic variables and late wood and total ring indices are given as *r* values.

older than 200 years are rare and that regeneration of oaks started around 1850 when woody species were planted along field boundaries and served as a source of seeds for tree establishment along meadow margins or in temporally abandoned plots. For woody species three important changes took place in the White Carpathian meadows over the last 100 years. First, surrounding woods have become considerably denser due to the increasing availability of other sources of energy than wood, concurrent with abandonment of such traditional management techniques as coppicing during first half of the 20th century (Warren & Key 1991, Rackham 1998). Second, meadows on steep slopes were colonized by hawthorn and oak when traditional mowing and hay-making ceased in the second half of the 20th century. Third, the common view that scattered oaks were for centuries an integral part of meadows led conservationists to plant rows of solitary trees (mostly *Q. robur*), which reduce the risk of landslides occuring on the unstable non-forested slopes on flysch sediments.

Progressive encroachment by woody species led to mesoclimate amelioration, together with an elevated deposition of nitrogen and decreased meadow biomass removal during the 20th century. Oak trees become an integral part of the meadow complex, increasing its overall diverstity (Manning et al. 2006, 2009). For instance, the many herbaceous plants that grew beneath the oaks provided seeds that germinated in the surrounding meadows (Klimeš 1995). Their importance as seed sources has dramatically increased over the last two decades with the implementation of new agrienvironmental schemes (Konvička et al. 2008) consisting of uniform machine mowing, usually done over a period of a few days, which prevents many of the herbaceous plants from ripening their seed. Oaks host the richest fauna of saproxylic insect, and especially sun-exposed dead wood of old solitery trees is one of the richest habitat in specialized invertebrates in Europe (Vodka et al. 2009). The grassland mycoflora is much enriched by the presence of scattered oaks as many species are symbiotically associated with their roots (Jongepier & Jongepierová 2001). However, these biodiversity hotspots are now threatened by an increased mortality and poor recruitment of oaks, which is often associated with intensive land use (Laanelaid et al. 2008). Our results indicate that a decrease in rainfall and increase in summer temperatures over the last decades (1970s–1990s was the longest driest interval in the last 150 years) could be responsible for the high number of oaks that are dying prematurely in this region. The prolonged periods of unfavourable conditions for growth, such as those in 1990s (Helama et al. 2009), cause the oak trees to become more prone to fungal attack and mistletoe (*Loranthus europaeus*) hemiparasites (Glatzel 1983), which predisposes them to damage or death (Thomas et al. 2002).

A distinct association of climate with different components of radial growth is reported here. Early wood increments are more associated with the previous years' autumn temperature than rainfall, while late wood increments are more closely associated with rainfall than temperature in the current growing season. Similar associations are documented for oaks in the UK (Pilcher & Gray 1982), southern Poland (Bednarz & Ptak 1990), nothern Spain (Rozas 2005), western France (Lebourgeois et al. 2004), Estonia (Laanelaid et al. 2008), southern Slovenia (Čufar et al. 2008), southern Finland (Helama et al. 2009) and Sweden (Drobyshev et al. 2008), indicating that the radial growth of pedunculate and sessile oaks may be limited by water stress throughout Europe. Increase in the width of early wood is associated with the occurrence of a warm October and November the previous year, probably linked to the late onset of winter, reducing respiration and increasing assimilation of food and storage of assimilates (Barbaroux & Bréda 2002), and thus a higher potential for rapid cambial growth the following year (Fritts 1976). Our results also indicate that above-normal temperatures in late winter (February) and early spring and below-normal spring rainfall (April) are associated with increased early wood formation. Many studies done in temperate climates report a strong positive association between high spring temperatures and radial growth (the time of early wood formation); the explanation given is that favourable conditions for photosynthesis early in a growing season result in early initiation of cambial activity and increased supply of photosynthates, which benefits cell-wall thickening later in the season (Misson et al. 2004). High soil temperatures in the late winter/early spring period may encourage root growth (Cherubini et al. 2003), which is advantageous when the summers are dry. The water in deeper horizons of the soil can be readily available because these horizons are not frozen or higher soil temperatures may enhance water uptake (Kramer & Kozlowsky 1979). Root growth in oaks occurs when winter temperatures are slightly above 0° C (Hoffmann 1974). In the study area, mean February temperatures ranged between 5.5 to –10.9 °C during the period 1941–2007 (records from the nearby Strážnice meteorological station), with a substantial increase since mid 1980s (–0.5 °C mean temperature for the period 1940–1985 vs. 0.4 °C for the period 1986–2007).

Many dendroclimatic studies record that ring width in warm and dry climates are positively associated with summer rainfall and negatively with summer temperature (Fritts 1976). The positive association of ring width with May and June rainfall and negative association with June temperature in our dataset indicate that increased growth was associated with cool, humid and therefore relatively moist weather in these months. Even if ring growth in both species is associated positively with high May–June rainfall and driven by similar climatic factors, our results indicate certain differences, which can be ascribed to their different site (soil moisture) requirements (Tyree & Cochard 1996). Decrease in ring growth in pedunculate oak, which is typical of rich, humid sites in the lowlands, was associated with rainy/cool Aprils (delaying the onset of growing season) and hot Junes (causing short-term droughts). For sessile oak, which has its growth optima on poor, dry sites in the upland areas, ring growth was not associated with the climate in these months, which might indicate it is better adapted to adverse conditions in late spring and summer. The study site is a wind exposed west-facing slope on impermeable calcareous clay and sandstone bedrock, which results in rapid surface runoff, and is frequenly subjected to extreme climatic conditions. Moreover, most of the area is subject to water erosion and landslides are common (Jongepier & Jongepierová 2001). Pedunculate oak is known to be more vulnerable than sessile oak to summer-drought induced cavitation, stops growth at a lower water stress, suffer a greater mortality after a period of drought, and the resistance to water flow in its shoots with a basal diameter of 20–25 mm is greater (Tyree & Cochard 1996). The mid August measurements of the water content of the leaves at our study site were higher for pedunculate than sessile oak (Mazůrek 2008), indicating a larger need for water. Hence, the recent summer droughts could have rendered pedunculate oak more sensitive to exogenous factors, including winter frost, tracheomycosis and mistletoe infection, especially solitary trees for which extreme conditions are not ameliorated by surrounding trees. This accords with the results of a survey of the health of closed canopy and scattered trees in the study region (Mazůrek 2008), which revealed that there is a greater incidence of crown dieback (> 50%) and mistletoe infections (> 5 clumps per tree) in scattered pedunculate oaks (Fig. 1), which presumably suffer more from extreme conditions than shaded trees.

The pointer year analysis shows that extremely thin tree-rings are associated with dry and hot periods, whereas the production of extremely wide tree-rings is associated with wet and cool periods. Similar growth anomalies associated with extreme May–June rainfall are recorded for *Abies alba* in southern Moravia (Brázdil et al. 2002). In this context it is of interest that fir, sessile and pedunuculate oaks grew less in the late 1970s, when there was a prolonged drought. In northern Germany, the droughts between 1976 and 1983 predisposed sessile and pedunculate oaks to subsequent frost damage in the winters of 1984–1987 (Hartmann et al. 1989, Hartmann & Blank 1992). In general, the pointer years for southern Moravian oaks tend to coincide with the pan-European oak growth anomalies recorded in the dry years of 2003, 1992, 1983, 1979, 1976, 1973, 1935, 1928 and 1908 and the wet years of 1969 and 1959 (Lebourgeois et al. 2004, Čufar et al. 2008, Helama et al. 2009). In some years, severe droughts or abundant rainfall are associated with narrow or wide rings, respectively, but they are not defined as pointer years because less than 70% of the trees exhibited either a positive or negative change in growth. This was the case for the positive years 1965, 1939, 1926 and 1910.

Many of the negative growth anomalies, however, are not associated only with rainfall extremes at the time of late wood formation. Many thin tree-rings are associated with a very dry or cold winter/spring resulting in low snow melt and subsequent water shortages during early wood formation, followed by a cool and wet April (hampering the onset of late wood growth), and a hot and dry May and June. This was particularly marked in the years 2003, 1979, 1973, 1956 and 1947. Extremely low air temperatures in winter are associated with the production of narrow rings by fir trees in southern Moravia, mainly in years when there is little snow cover at dry sites (Brázdil et al. 2002), as was the case in the severe winters of 1928/29 and 1962/63. A similar reduction in growth was not recorded in the oaks studied, although in other years low winter temperatures were associated with larger reductions in growth (1979, 1956, 1901, 1947, 1922). Interestingly these years were preceded by periods of severe droughts (1976–1978, 1946, 1920–1921), whereas rainfall and temperatures in the summers preceding the severe winters of 1928/29 and 1962/63 were normal. These findings accord with previous studies done throughout Europe. Recently, Helama et al. (2009) record that summer droughts in Finland predispose poorly acclimatized pedunculate oaks to be more sensitive to low February temperatures and suffer frost damage to their roots; however, trees growing at less water-limited sites on deeper soils are not so affected. Thomas & Ahlers (1999) found that previous summer droughts diminish the frost hardiness of the bark of pedunculate oak, thereby increasing the risk of frost damage.

Conclusions

This is the first comparative dendrochronological study of two species of oak in southern Moravia, Czech Republic. The association between climate and yearly variation in the radial growth of pedunculate (*Quercus robur*) and sessile (*Q. petraea*) oak in the White Carpathians was assessed. This mountain range is renowned for its high plant and insect diversity, and savanna-like grasslands with scattered oak trees, many of which have died of causes other than natural senescence over the last two decades. Extreme climatic events, such as summer drought, are thought to be responsible for the decline of oak. This idea was tested by comparing late wood, early wood and total ring widths with monthly climatic data over the period 1900–2006, using a combination of a response function and pointer year analyses, which provided comprehensive dendroclimatological information. The two approaches clearly indicated that early wood increments were more associated with the autumn and winter temperatures of the previous year, while late wood increments were more closely associated with rainfall in the current growing season. A shortage of water, due to low rainfall and high temperatures during the period of late wood formation (May–June), was negatively associated with late wood growth and hence the total annual growth increment. The increase in summer temperatures and frequent occurrence of severe summer droughts over the last three decades are negatively associated with radial stem growth in the White Carpathian oak population and may have contributed to their recent decline in abundance.

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Souhrn

Dub letní (*Quercus robur* L.) a dub zimní (*Q. petraea* L.), dominantní druhy evropských listnatých lesů, ustupují v mnoha regionech napříč Evropou. Extrémní klimatické výkyvy (letní sucha, zimní mrazy) jsou považovány za klíčové faktory způsobující toto odumírání v důsledku negativního vlivu na proces formování dřeva. Na základě rozsáhlého odběru vzorků z dubů rostoucích solitérně nebo v malých lesících v savanovité krajině druhově bohatých luk Bílých Karpat, nejzápadnějšího výběžku Karpat v jihovýchodní části České republiky, jsme chtěli zjistit, jak je šířkový přírůstek kmenů ovlivněn klimatickými výkyvy během posledních 100 let. Vliv klimatu byl hodnocen srovnáním šířky letokruhů jarního a letního dřeva a celkového přírůstu s klimatickými daty za období let 1900–2006, použitím kombinace tzv. funkce odezvy (metody založené na mnohonásobné regresi) a analýzy extrémních letokruhů. Tyto dva přístupy ukazují, že růst letního dřeva dubů rostoucích v hlubokých, na vápník bohatých půdách, které v létě vysychají, je většinou řízen současnou vodní bilancí v květnu až červnu, zatímco růst jarního dřeva je ovlivněn klimatickými podmínkami v předcházejícím podzimu a zimními teplotami. Extrémní růstové roky se shodují s abnormálně vlhkým nebo suchým květnem až červnem, obvykle následovanými chladným nebo horkým červnem. Deficit vodní bilance jako následek nízkých srážek a vysoké teploty během léta negativně ovlivnil formování letního dřeva a tím i celkový roční radiální přírůstek. Tyto výsledky podporují představu o klíčové roli klimatických změn (nedostatek srážek a rostoucí letní teploty během posledních tří dekád) v procesu vedoucímu k odumírání vysokého počtu dubů na bělokarpatských loukách. Dlouhá perioda nepříznivých klimatických podmínek způsobuje, že oslabené duby jsou náchylnější k infekci houbovými chorobami a ochmetem, což vede k dalšímu oslabení nebo smrti, zvláště u soliterně rostoucích dubů letních.

References

Barbaroux C. & Bréda N. (2002): Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ringporous sessile oak and diffuse-porous beech trees. – Tree Physiol. 22: 1201–1210.

Bednarz Z. & Ptak J. (1990): The influence of temperature and precipitation on ring widths of oak (*Quercus robur* L.) in the Niepolomica forest near Cracow, Southern Poland. – Tree-Ring Bull. 50: 1–10.

Biondi F. (1997): Evolutionary and moving response functions in dendroclimatology. – Dendrochronologia 15: 139–150.

Biondi F. & Waikul K. (2004): DENDROCLIM 2002: a C++ program for statistical calibration of climate signals in treering chronologies. – Computers and Geosciences 30: 303–311.

Brázdil R., Štěpánková P., Kyncl T. & Kyncl J. (2002): Fir tree-ring reconstruction of March–July precipitation in southern Moravia (Czech Republic). – Clim. Res. 20: 223–239.

Butin H. (1995): Tree diseases and disorders: causes, biology and control in forest amenity trees. – Oxford Univ. Press, Oxford.

Cherubini P., Gartner B. L., Tognetti R., Bräker O. U., Schoch W. & Innes J. L. (2003): Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. – Biol. Rev. 78: 119–148.

Cook E. R. (1985): A time series analysis approach to tree-ring standardization. – PhD Thesis, Univ. Arizona, Tucson.

Cook E. R. & Kairiukstis L. A. (1990): Methods of dendrochronology: applications in the environmental sciences. – Kluwer, Dordrecht.

Čufar K., De Luis M., Eckstein D. & Kajfež-Bogataj L. (2008): Reconstructing dry and wet summers in SE Slovenia from oak tree-ring series. – Int. J. Biometeorol. 52: 607–615.

Di Filippo A., Biondi F., Čufar K., de Luis M., Grabner M., Maugeri M., Saba E. P., Schirone B. & Piovesan G. (2007): Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. – J. Biogeogr. 34: 1873–1892.

Dimopoulos P., Bergmeier E., Chytrý M., Rodwell J., Schaminée J. & Sýkora K. (eds) (2005): European oak woodlands: past, present and future. – Botanika Chronika 18: 1–316.

Drobyshev I., Linderson H. & Sonesson K. (2007): Temporal mortality pattern of pedunculate oaks in southern Sweden. – Dendrochronologia 24: 97–108.

Drobyshev I., Niklasson M., Eggertsson O., Linderson H. & Sonesson K. (2008): Influence of annual weather on growth of pedunculate oak in southern Sweden. – Ann. For. Sci. 65: 512.

Dwyer J. P., Cutter B. E. & Wetteroff J. J. (1995): A dendrochronological study of black and scarlet oak decline in the Missouri Ozarks. – For. Ecol. Manage. 75: 69–75.

Fritts H. C. (1976): Tree-rings and climate. – Academic Press, New York.

Gibbs J. N. & Greig B. J. W. (1997): Biotic and abiotic factors affecting the dying-back of pedunculate oak *Querus robur* L. – Forestry 70: 399–406.

Glatzel G. (1983): Mineral nutrition and water relations of hemiparasitic mistletoes: a question of partitioning: experiments with *Loranthus europaeus* on *Quercus petraea* and *Quercus robur*. – Oecologia 56: 193–201.

Guiot J. (1991): The bootstrapped response function. – Tree-Ring Bull. 51: 39–41.

Hartmann G. & Blank R. (1992): Winterfrost, Kahlfrass und Prachtkäpferbefall als Faktoren im Ursachenkomplex des Eichensterbens in Norddeutschland. – Forst Holz 47: 443–452.

Hartmann G., Blank R. & Lewark S. (1989): Eichensterben in Norddeutschland: Verbreitung, Schadbilder, mögliche Ursachen. – Forst Holz 44: 475–487.

Helama S., Laanelaid A., Raisio J. & Tuomenvirta H. (2009): Oak decline in Helsinki portrayed by tree-rings, climate and soil data. – Plant Soil 319: 163–174.

Hoffmann G. (1974): Beendigung des Wurzelwachstums in der Vegetationsperiode und Zuwachs von Wurzeln im Winter. – Beitr. Forstw. 3: 38–41.

Holmes R. L. (1994): Dendrochronology program library, laboratory of tree-ring research. – Univ. Arizona, Tucson.

Jensen M. E. & Haise H. R. (1963): Estimating evapotranspiration from solar radiation. – J. Irrigat. Drain. Div. 89: 15–41.

Jongepier J. W. & Jongepierová I. (2001): Flower meadows of the Czech White Carpathians: reviving a symbiosis between nature and humans. – The Open Country 3: 37–44.

Jongepierová I. (ed.) (2008): Louky Bílých Karpat [Grasslands of the White Carpathian mountains]. – ZO ČSOP Bílé Karpaty, Veselí nad Moravou.

Jung T., Blaschke H. & Neumann P. (1996): Isolation, identification and pathogenicity of *Phytophthora* species from declining oak stands. – Eur. J. For. Pathol. 26: 253–272.

Klimeš L. (1995): Small-scale distribution of species richness in a grassland (Bílé Karpaty Mountains, Czech Republic). – Folia Geobot. Phytotax. 30: 499–510.

Klimeš L. (1999): Small-scale plant mobility in a species-rich grassland. – J. Veg. Sci. 10: 209–218.

Konvička M., Beneš J., Čížek O., Kopeček F., Konvička O. & Vitaz L. (2008): How too much care kills species: grassland reserves, agrienvironmental schemes and extinction of *Colias myrmidone* (*Lepidoptera*: *Pieridae*) from its former stronghold. – J. Insect. Cons. 12: 519–525.

Králíček M. & Gottwald A. (1984): Motýli jihovýchodní Moravy I. [Butterflies of Southeast Moravia I.]. – Museum Uherský Brod & OV ČSOP, Uherské Hradiště.

Kramer P. J. & Kozlowsky T. T. (1979): Physiology of woody plants. – Academic Press, New York.

Laanelaid A., Sohar K. & Meikar T. (2008): Present state and chronology of oaks in an oak forest in Saaremaa Island, Estonia. – Baltic Forestry 14: 34–43.

Lebourgeois F., Cousseau G. & Ducos Y. (2004): Climate-tree-growth relationships of *Quercus petraea* Mill. stand in the Forest of Bercé ("Futaie des Clos", Sarthe, France). – Ann. For. Sci. 61: 361–372.

Manning A. D., Fischer J. & Lindenmayer D. B. (2006): Scattered trees are keystone structures implications for conservation. – Biol. Conserv. 132: 311–321.

Manning A. D., Gibbons P. & Lindenmayer D. B. (2009): Scattered trees: a complementary strategy for facilitating adaptive responses to climate change in modified landscapes? – J. Appl. Ecol. 46: 915–919.

Mazůrek P. (2008): The woody plants in mown meadows: the analysis of morphology, age, growth and survival of trees on species-rich meadows in the White Carpathian Mts. – Bc. Thesis, Univ. South Bohemia, České Budějovice.

Misson L., Rathgeber C. & Guiot J. (2004): Dendroecological analysis of climatic effects on *Quercus petraea* and *Pinus halepensis* radial growth using the process-based MAIDEN model. – Can. J. For. Res. 34: 888–898.

Pilcher J. R. & Gray B. (1982): The relationships between oak tree growth and climate in Britain. – J. Ecol. 70: 297–304.

Rackham O. (1998): Savanna in Europe. – In: Kirby K. J. & Watkins C. (eds), The ecological history of European forests, p. 1–24, CABI, Wallingford.

Rozas V. (2005): Dendrochronology of pedunculate oak (*Quercus robur* L.) in an old-growth pollarded woodland in northern Spain: tree-ring growth responses to climate. – Ann. For. Sci. 62: 209–218.

Schweingruber F. H. (1996): Tree-rings and environment: dendroecology. – Haupt, Berne.

Siwecki R. & Ufnalski K. (1998): Review of oak stand decline with special reference to the role of drought in Poland. – Eur. J. For. Pathol. 28: 99–112.

Thomas F. M. & Ahlers U. (1999): Effects of excess nitrogen on frost hardiness and freezing injury of aboveground tissue in young oaks (*Quercus petraea* and *Q. robur*). – New Phytol. 144: 73–83.

Thomas F. M., Blank R. & Hartmann G. (2002): Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. – For. Pathol. 32: 277–307.

Tyree M. T. & Cochard H. (1996): Summer and winter embolism in oak: impact on water relations. – Ann. For. Sci. 53: 173–180.

UNEP (1992): World atlas of desertification. – Edward Arnold, London.

Vodka S., Konvička M. & Čížek L. (2009): Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. – J. Insect. Cons. 13: 553–562.

Wargo P. M., Houston D. R. & LaMadeleine L. A. (1983): Oak decline. – USDA Forest Service For. Ins. & Dis. Leaflet 165, Forest Service, Washington, DC.

Warren M. S. & Key R. S. (1991): Woodland: past, present and potential for insect. – In: Collins M. N. & Thomas J. A. (eds), The conservation of insects and their habitats, p. 155–210, Academic Press, London.

Zhang S. Y. (1997): Variations and correlations of various ring width and ring density features in European oak: implications in dendroclimatology. – Wood Sci. Technol. 31: 63–72.

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