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EXPLORING GROWTH VARIABILITY AND CROWN VITALITY OF SESSILE OAK (*QUERCUS PETRAEA*) IN THE CZECH REPUBLIC

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Abstract: Unraveling climatic effects on growth of oak — Europe's most ecologically and economically important forest species — has been the subject of many recent studies; however, more insight based on field data is necessary to better understand the relationship between climate and tree growth and to adapt forest management strategies to future climate change. In this report, we explore the influence of temperature, precipitation and drought variability on the productivity and vitality of oak stands in the Czech Highlands. We collected 180 cores from mature oaks (*Quercus petraea*) at four forest stands in the Czech Drahany Highlands. Standard dendro-methods were used for sample preparation, ring width measurements, cross-dating, chronology development, and the assessment of growth-climate response patterns. Crown vitality was also evaluated, using the modified ICP Forests methodology. Late spring precipitation totals between May and June as well as the mean July temperature for the year of ring formation were found to be the most important factors for oak growth, whereas crown condition was significantly affected by spring and summer drought. This study is representative for similar bio-ecological habitats across Central Europe and can serve as a dendroclimatological blueprint for earlier periods for which detailed meteorological information is missing.

Keywords: Central Europe, crown condition, precipitation, sessile oak, temperature, tree rings.

1. INTRODUCTION

Climate is one of the most important drivers of tree growth (Fritts, 1976; Schweingruber, 1996). Understanding the effects of climate, including variations in mean temperature and total precipitation, on oak radial increment has recently been the subject of many European studies (Lebourgeois *et al.*, 2004; Friedrichs *et al.*, 2009; Tegel *et al.*, 2010; Mérian *et al.*, 2011; Petráš and Mecko, 2011; Bronisz *et al.*, 2012). However, assessments of the relationship between crown condition and radial increment currently remain underrepresented (e.g., Drobyshev *et al.*, 2007).

As a result of the subsidy state policy in the Czech Republic, there has been a gradual decrease in the area

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covered by coniferous species with areas of broadleaved species, especially oak and beech. Oak is the second most economically important broadleaved species in forest management in the Czech Republic (MZe ČR, 2012). Up to this point, oak tree-ring research in the Czech Republic has not been given sufficient attention, and the only available studies are recent. Some of the studies that do exist have addressed the following: wood increments during a growing season in a floodplain for English oak (Horáček *et al.*, 2003); the effects of climate on the formation of early- and latewood, with tree-ring width and oak wood density determined using both English and sessile oak in south Moravia (Doležal *et al.*, 2010; Vavrčík and Gryc, 2012); the growth response of sessile oak to climate and hydrology changes in the Zbytka Nature Reserve (Čejková and Poláková, 2012); and the creation of an oak tree-ring chronology for the Czech Republic (Kolář *et al.*, 2012). However, this oak tree-ring chronology does not have sufficient sample depth of tree-ring series in the most recent period, *i.e.* the period important for proxy data (ring width) calibration with instrumental weather data, which can serve for the reconstruction of climatic conditions of the past (Büntgen *et al.*, 2010). Except for monitoring within the ICP Forests network (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests operating under the UNECE Convention on Long-range Transboundary Air Pollution), oaks in the Czech Republic have not been given a great deal of attention, especially regarding crown condition monitoring and its possible use and interpretation.

The diagnosis of tree vitality or health is only possible if a combination of tree-ring research and crown assessment is used. The response of radial growth and defoliation (as the main parameter of crown condition assessment) may occur with different delays. In some cases, the first observable reaction to an occurring factor is defoliation (e.g., when insects feed on the crown), while the radial growth response is delayed; in other cases (e.g., extreme drought), the growth reduction is immediate, whereas the reduction in foliage can be observed several months later (Schweingruber, 1996).

Studying the effect of climate on the growth and vitality of oaks and their stands in upland and highland areas, which form a substantial amount of the Czech Republic territory, will strongly contribute to the process of creating guidelines for forest management and biological conservation, as well as the formulation of necessary adaptation measures in response to a changing climate and associated ecological alternations.

The aim of this study is to make a unique connection between the dendroclimatological analysis and the evaluation of crown condition of the sessile oak (*Quercus petraea*) in the central part of the Drahany Highlands in the Czech Republic that is representative of typical sessile oak production area in the broader area. No similar extensive study has been performed on this topic (this number of oaks and of precisely calculated climatic indexes for chosen areas) in Central Europe. The results of this study can be generalized for similar areas not only in the Czech Republic but also in Central Europe as a whole. Tree-ring series will be added to the oak tree-ring chronology for the Czech Republic, improving its replication for the last 150 years, *i.e.* the period where the sample depth is insufficient so far.

2. MATERIALS AND METHODS

Study area

This research was conducted in four forest stands with a predominance of oak in the central part of the Drahany Highlands near Brno, Czech Republic, in 2011 and 2012. The selected stands were typical for the oak forest ecosystems found in thirteen Czech Natural Forest Areas (**Fig. 1**). Nature Forest Areas are territorial units delineated primarily by three characteristics: i) substantial differences in parent material, which affects the key soil characteristics; ii) differences in the terrain configuration; iii) differences in micro- and meso-climate and, thus, in the occurrence of forest communities.

All trees within the stands were 120 to 140 years old and were located at altitudes from 425 m a.s.l. to 460 m a.s.l. (**Table 1**). The region is relatively moist, with an average annual precipitation of 625 mm, and the average annual temperature during the 1961–2001 monitoring period was 8.7°C. Soil conditions are very similar — the prevailing soil type is cambisol. The pedogenetic matrix is granodiorite (phaneritic texture intrusive igneous rock). All plots (stands) are in the Fagus–Quercus forest vegetation zone (Viewegh *et al.*, 2003).

Methods

Samples were extracted using a Pressler borer at breast height along the contour line so that the increments were not influenced by the presence of tension wood.

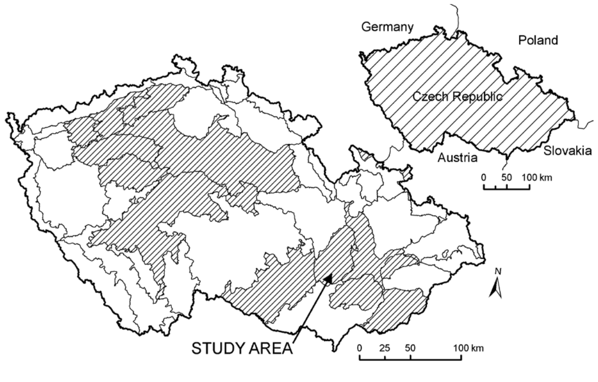

Fig. 1. *Location of the study area within the Central Europe and Natural Forest Areas. Areas with sites and oak forest ecosystems similar to the selected stands are shaded.*

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Table 1. *A detailed overview of the study area.*

Plot sign	GPS data	Altitude (m a.s.l.)	Slope gradient (degree)	Slope orientation	Edaphic category	Age in 2012	% of oak	Other woody plant species	Herb layer	
									Cover (%)	Eudominant species
1	N49 16 22.044 E16 38 32.471	425	5	S	illimerosa trophica	120	73	*Carpinus betulus, Tilia cordata, Fagus sylvatica*	20%	*Carex pilosa*
2	N49 16 53.419 E16 37 47.178	460	10	SW	trophica	136	87	*Carpinus betulus*	90%	*Poa nemoralis, Melica nutans, Convallaria majalis*
3	N49 16 42.438 E16 37 31.174	430	10	W	mesotrophica	129	70	*Carpinus betulus, Fagus sylvatica*	90%	*Poa nemoralis, Luzula luzuloides*
4	N49 17 5.639 E16 37 25.650	440	7	SW	illimerosa trophica	131	59	*Carpinus betulus, Tilia cordata, Fagus sylvatica*	40%	*Carex pilosa, Poa nemoralis*

Forty-five samples were taken at each plot for dendrochronological analyses (180 in total), with one sample taken from each tree. The wood samples were measured using the VIAS TimeTable measuring system, and the measurement and synchronization of tree-ring sequences were carried out using PAST4 (©SCIEM). The annual wood increments were measured to 0.01 mm accuracy. When a set of wood samples was processed, the individual tree-ring series were cross-dated. The tree-ring series, which correlated significantly at the 99% confidence limit, were used to create an average tree-ring series. The degree of similarity between the tree-ring series was assessed using the correlation coefficient, the coefficient of agreement (Eckstein and Bauch, 1969), and an optical comparison of both series, which is crucial for the final dating (Rybníček *et al.*, 2010).

The growth trends of individual tree-ring series and their autocorrelation structures were removed by the ARSTAN application (Grissino–Mayer *et al.*, 1992) using a single detrending method (**Fig. 2**) (Holmes *et al.*, 1986) — a negative exponential function (Fritts *et al.*, 1969). The regional index residual of the tree-ring chronology was created using the ARSTAN application. Out of the 180 cores, 158 tree-ring series were used for the creation of the regional tree-ring chronology (several samples were removed); the resulting regional tree-ring chronology spanned from 1867 to 2011 (**Fig. 3**). DendroClim2002 was used to model the radial increments in dependence on climatic characteristics (Biondi and Waikul, 2004).

Climatic data were derived for the location defined by geographic coordinates 49°16'53.419"N, 16°37'47.178"E and 460 m a.s.l. altitude, based on interpolation from a set of nearby weather stations, applying locally weighted regression and accounting for the effect of altitude. The original station series measurements were subjected to quality control and homogenization using ProClimDB (Štěpánek, 2007) and included 268 meteorological and 787 precipitation stations representing the territory of the Czech Republic. The database for the area of interest included daily data on minimum and maximum temperature, precipitation and global radiation sums, as well as daily mean wind speed and water vapor pressure. Using AgriClim (Trnka *et al.*, 2012) and SoilClim (Hlavinka *et al.*, 2011) software packages, daily soil water contents in two layers (0–0.4 and 0.4–1.3 m below soil surface) were calculated, as well as values of the standard precipitation index (SPI) according to McKee *et al.* (1993), the self-calibrated Palmer drought severity index (PDSI) and the Palmer Z-index (ZIND) according to Palmer (1965), as well as the standardized precipitation evapotranspiration index (SPEI) according to Vicente-Serrano *et al.* (2010).

The residual oak chronology and climatic time-series from 1961–2011 were used to calculate correlation coefficients between radial increments and climatic drivers. The correlation coefficients were calculated for a seasonal window from April of the previous year until September of the year of tree-ring formation (referred to as "the given year"), *i.e.*, for a period of 18 months, as this interval should have the highest influence on the radial increment. The correlations of the given year were also calculated for April to May (when earlywood is assumed to be formed), April to September (the growing season), May to September (when latewood forms), and June to August (typical summer months); additionally, correlations were analyzed for July to September of the previous year (thought to be a period of energy reserve formation for the next season).

Statistical comparison of radial increment and climatic factor time-series will allow us to determine the average long-term influence of the studied climatic parameters on the increments. Long-term climatic changes that may also affect tree growth do not have to be demonstrated in the correlation analysis to a statistically significant degree (Kienast *et al.*, 1987); to establish these effects, negative pointer years were analyzed. A negative pointer year is defined as an extremely narrow tree ring with growth reduction exceeding 40% compared with the average tree-ring width in the previous four years; this strong increment reduction is found in at least 20% of the trees from this area (Schweingruber *et al.*, 1990). Negative pointer years were divided into four groups for better

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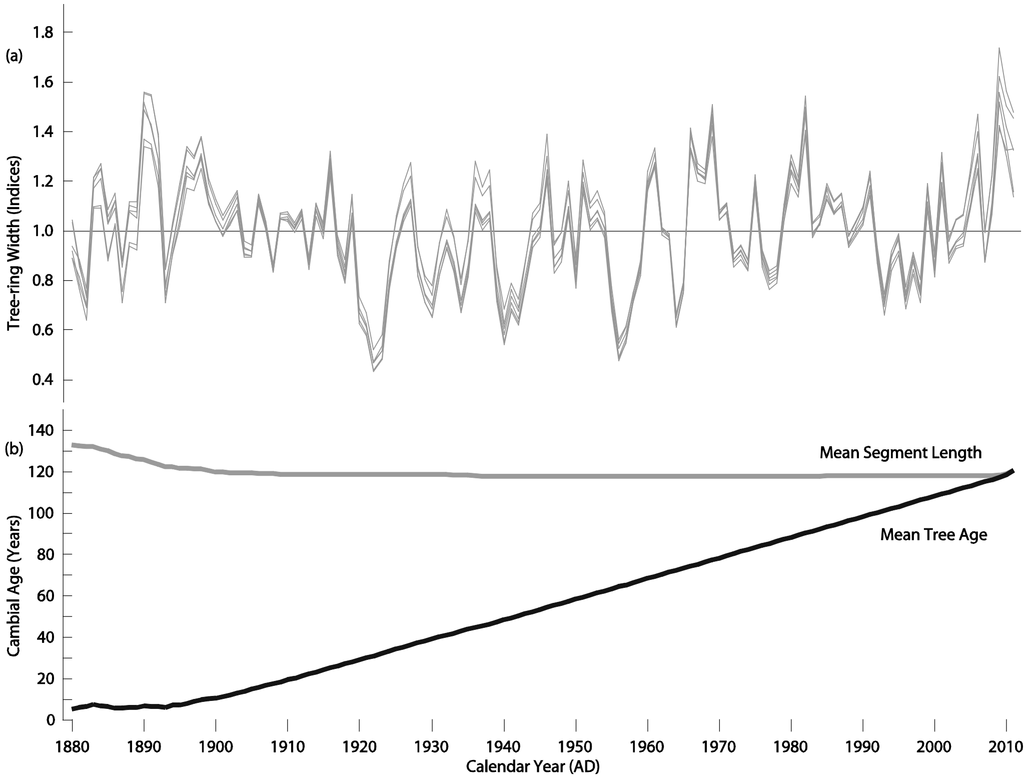

Fig. 2. *(a) Six slightly different oak chronology versions after truncation at a minimum replication of 10 series, and (b) associated temporal changes in mean segment length and mean tree age. For chronology development, we used three different standardization techniques: Cubic smoothing splines with 50% frequency cut-off at 150 years, negative exponential functions and RCS. For index calculation we used ratios and residuals after power-transformation.*

orientation based on the percentage of trees responding negatively in a particular year.

Oak crowns of 20 trees were evaluated using binoculars based on ground observation for three of the monitored stands. We could not conduct the evaluation in the fourth stand as felling was in progress during the time of our evaluation. Our methodology complies with the ICP Forests evaluation methodology (Eichhorn *et al.*, 2010), but the parameters were modified based on our experience with evaluating crown transformation using the Norway spruce methodology (Cudlín *et al.*, 2001). By expanding the methodology, we aimed to capture adaptation processes occurring in the crown. The parameters of the crown condition are shown in **Table 2**, and all parameters assessed in percentages were assessed using an estimate step of 5%.

Tree crown parameters were compared with tree-ring width using the width of the last tree ring and the mean width of the last ten rings. With respect to the effect of *Tortrix viridiana* feeding on current defoliation, we used parameters that capture long-term processes in the crown, *i.e.*, relative crown height (% of crown height within the tree height) and the proportion of secondary shoots.

3. RESULTS

The regional tree-ring chronology generated in this study spans 1867 to 2011. The temporal distribution of the 158 individual oak samples reveals a robust coverage during the past 120 years, during which high EPS (>0.95) and Rbar values (>0.45) were stable (**Fig. 3**). Comparing six slightly different tree-ring chronologies after applying various detrending techniques indicates the reliability of our data over time (**Fig. 2**); in fact, applying different detrending techniques did not affect the overall shape of the resulting chronologies.

The results of analyzing the radial increment response to the climate condition are shown in **Table 3**. The correlation of the radial increment with mean monthly temperature is negative and statistically significant for July of the previous year as well as January and July of the given year (the year of ring growth). This suggests that summer temperatures that are warmer than usual during the preceding season and winter tend to negatively affect growth. The positive effect of increased temperature in September suggests that oak benefits from a longer growing season. The results show a positive relationship be-

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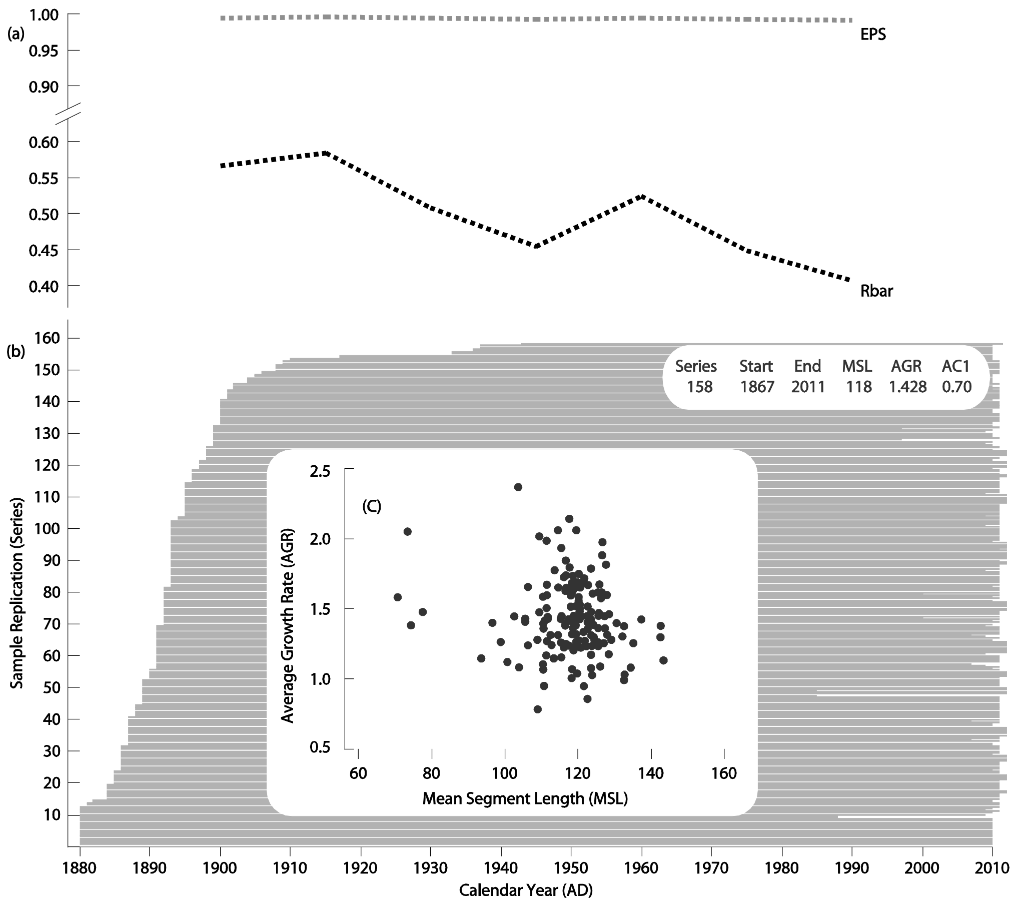

Fig. 3. *(a) Expressed Population Signal (EPS) and inter-series correlation (Rbar) of (b) the 158 oak ring width measurement series, and (c) showing the relationship between average growth rate (AGR) and mean segment length (MSL) of individual core samples. EPS and Rbar statistics were calculated over 30-year windows lagged by 15 years. The upper right inset provides insight into data characteristics.*

Table 2. *Parameters of the crown condition assessment.*

Parameter	Specifications, values
Social class	1 = dominant, 2 = codominant, 3 = subdominant, 4 = suppressed
Proportion of parts of the crown	% of tree height: part A, from the top to the first branching of at least 2nd order; part B, from the first branching of at least 2nd order to the last branching of 1st-order branches; part C, from the last branching of 1st-order branches to the last bottom-most branch on the stem
Defoliation	% in all three parts of the crown
Proportion of dead branches	% of all branches in the three parts of the crown
Type of crown damage	4 types: transparent damage, small windows, large windows with secondary shoots, and large windows without secondary shoots; proportion of the damage in % of the crown volume
Proportion of secondary or shortened shoots within all shoots	% for all three parts of the crown
Type of stem damage	Unique necrotic wounds, small wounds up to 1 cm in size, larger wounds to the xylem, damage affecting the xylem, large wounds deforming the stem and branches
Presence of insect pests and pathogenic fungi	Scientific name, character of damage
Discoloration	Color and % proportion of the crown parts A + B
Proportion of reduced leaves	% of leaves with an area reduced by at least 50% in crown parts A+B
Flowering	0 = absent, 1 = scarce, 2 = common, 3 = abundant
Fruiting	0 = absent, 1 = scarce, 2 = common, 3 = abundant

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Table 3. *Values of correlation coefficients of the regional residual index tree-ring chronology with* T_{avg} *= average monthly temperature,* T_{max} *= average monthly maxima temperature,* T_{min} *= average monthly minimum temperature, aVP = actual water vapor pressure, VPD = Vapor pressure deficit, RH = Relative humidity, 1 m SPI = 1 month standardized precipitation index, 3 m SPI = 3 month standardized precipitation index, 12 m SPI = 12 month standardized precipitation index, 1 m SPEI = 1 month standardized precipitation evapotranspiration index, 3 m SPEI = 3 month standardized precipitation evapotranspiration index, 12 m SPEI = 12 month standardized precipitation evapotranspiration index, ZIND = Palmer Z-index, PDSI = Palmer drought severity index, AWR 0–40 = relative saturation of soil profile by soil water in the top 40 cm, AWR 40–130 = relative saturation of soil profile by soil water from 40 to 130 cm, AWR = relative saturation of soil profile by soil water from top to 130 cm depth, from July of the previous year (P) to September of that particular year and the period July–September (7–9 P) of the previous year and the period April–May, April–September, May–September, Jun–August of that particular year for the period of 1961–2011. Values highlighted are statistically significant (- = negative correlation) (α = 0.05).*

	7P	8P	9P	10P	11P	12P	1	2	3	4	5	6	7	8	9	7–9P	4–5	4–9	5–9	6–8
T_{avg}	**-0.23**	-0.10	0.03	0.10	0.06	0.18	**-0.28**	-0.07	0.02	0.12	0.02	-0.10	**0.26**	-0.06	**0.38**	-0.15	0.08	0.17	0.17	0.07
T_{max}	**-0.29**	-0.11	-0.01	0.08	0.04	0.18	**-0.27**	-0.10	-0.03	0.16	-0.02	-0.15	0.20	-0.10	**0.38**	-0.20	0.09	0.14	0.11	0.00
T_{min}	-0.13	-0.07	0.09	0.10	0.08	0.16	**-0.27**	-0.03	0.09	0.04	0.06	-0.01	**0.32**	0.04	**0.29**	-0.06	0.06	0.22	0.24	0.17
aVP	-0.04	0.03	0.07	0.15	0.08	0.20	-0.24	-0.07	0.10	0.02	0.05	0.06	**0.49**	0.22	**0.31**	0.03	0.05	**0.37**	**0.39**	**0.36**
VPD	**-0.26**	-0.13	-0.05	-0.10	-0.05	-0.04	**-0.32**	-0.09	-0.09	0.17	-0.01	**-0.20**	0.05	-0.20	0.25	-0.21	0.08	-0.02	-0.06	-0.13
RH	**0.25**	0.12	0.07	0.17	0.06	0.19	**0.34**	0.05	0.12	-0.15	0.01	**0.23**	0.08	**0.25**	-0.09	0.19	-0.10	0.09	0.15	**0.24**
Precipitation	0.21	-0.14	0.09	-0.05	0.02	0.22	-0.06	0.13	0.16	-0.04	**0.26**	**0.30**	**0.40**	0.06	-0.12	0.10	0.19	**0.30**	**0.33**	**0.30**
1m SPI	**0.31**	-0.15	0.11	-0.03	-0.04	0.19	-0.14	0.07	0.25	-0.05	**0.27**	**0.30**	0.20	0.04	-0.18	0.17	0.16	0.25	**0.29**	**0.29**
3m SPI	0.22	0.06	0.11	-0.08	0.03	0.05	0.04	0.05	0.18	0.17	**0.36**	**0.33**	**0.40**	**0.28**	0.11	0.15	**0.30**	**0.39**	**0.40**	**0.40**
12m SPI	0.00	0.01	0.06	0.07	0.14	0.12	0.11	0.10	0.17	0.16	0.24	**0.33**	**0.34**	**0.37**	**0.34**	0.03	0.21	**0.36**	**0.39**	**0.40**
1m SPEI	**0.35**	-0.12	0.09	-0.06	-0.04	0.19	-0.12	0.14	0.21	-0.07	**0.25**	**0.31**	0.12	0.04	-0.25	0.20	0.12	0.14	0.20	**0.25**
3m SPEI	0.19	0.09	0.16	-0.09	-0.03	0.01	0.03	0.11	0.19	0.14	0.26	0.27	**0.33**	0.24	0.01	0.17	0.21	**0.28**	**0.28**	**0.32**
12m SPEI	-0.04	0.00	0.02	0.02	0.08	0.06	0.06	0.05	0.13	0.14	0.20	**0.30**	**0.28**	**0.29**	0.23	-0.01	0.18	**0.28**	**0.30**	**0.33**
ZIND	0.21	-0.07	0.11	-0.05	-0.03	0.16	-0.08	0.08	**0.23**	-0.04	0.24	**0.34**	0.22	0.15	-0.07	0.12	0.15	0.27	**0.31**	**0.33**
PDSI	-0.03	-0.04	-0.03	-0.06	-0.07	-0.04	-0.05	-0.04	0.09	0.03	0.13	0.18	0.18	0.22	0.18	-0.03	0.08	0.17	0.19	0.20
AWR 0–40	0.25	0.13	0.02	0.09	0.02	0.20	**0.30**	0.16	**0.36**	0.04	0.12	**0.25**	0.25	0.11	-0.02	0.19	0.10	0.22	0.23	**0.28**
AWR 40–130	-0.03	0.08	-0.06	0.01	0.05	0.02	0.10	0.15	0.26	**0.29**	0.20	0.16	**0.29**	**0.30**	0.11	0.00	**0.26**	**0.31**	**0.28**	**0.30**
AWR	0.08	0.11	-0.03	0.04	0.04	0.08	0.19	0.18	**0.34**	**0.25**	0.19	0.20	**0.29**	0.25	0.06	0.07	0.23	**0.30**	0.23	**0.31**

tween the actual water vapor pressure (aVP) and the radial increment in July and September, and a negative effect of water vapor pressure deficit (VPD) on growth during June. This can be interpreted as growth dependence on sufficient soil water content. Increased actual evapotranspiration (indicated by a higher aVP) increases growth, while increased dryness (indicated by high VPD) decreases growth. The correlation between radial increment and monthly precipitation is positive and weak but statistically significant for May, June, and July of the given year; this relationship is partly preserved in the one-month SPI values. Interestingly, when longer SPI integration periods are used, even tighter correlations show that the growth of oak at the given site is positively correlated with wetter than usual conditions during the growing season. Nearly identical results are obtained when the SPEI index is used. PDSI, the index that is most often used in drought climate reconstructions by dendroclimatologists, shows no significant correlations. It is also clear that the indicator for short-term drought (ZIND) is a more useful metric than the long-term PDSI index. This finding is likely caused by the relatively short record; PDSI was designed to capture prolonged drought events. Soil moisture content (AWR) shows a positive correlation with radial increment in nearly all months of the given or previous year, and the results are close to those of the 3-month SPEI and SPI.

The lowest radial increment was recorded in 1964 at the beginning of the correlation period; another more substantial drop in radial increment occurred in the 1970s and was only interrupted in 1975. The last, most significant decrease in radial increment is obvious between 1992 and 1998. In contrast, the greatest radial increment was recorded at the end of the monitored period, in 2009 (**Fig. 4**). The years with low increments were also confirmed by analyzing negative pointer years. During the most extreme years, 1964 and 1993, 92% and 67%, respectively, of the trees forming the tree-ring chronology responded negatively (**Table 4**).

The results of the crown condition assessments are presented in **Table 5**. The oaks in the three examined stands were strongly defoliated, with the highest levels of defoliation occurring in plot 3 and the lowest levels occurring in plot 1. The highest level of defoliation occurred in the central part of the crown (part B, from the first branching of at least 2nd-order branches to the last branching of 1st-order branches). The total defoliation in parts A and B (*i.e.*, from the top to the last branching of 1st-order branches) ranged from 30% (one tree in plot 2) to 95% (one tree in plot 3); the mean defoliation of all 60 trees was 54%, and the mean value for each stand is presented in **Table 5**. The highest proportion of dry branches was in the central part of the crown (B), with a minimum of 5% (one tree in plot 2) and a maximum of 60% (one tree in plot 3); the average defoliation was 21%. We also

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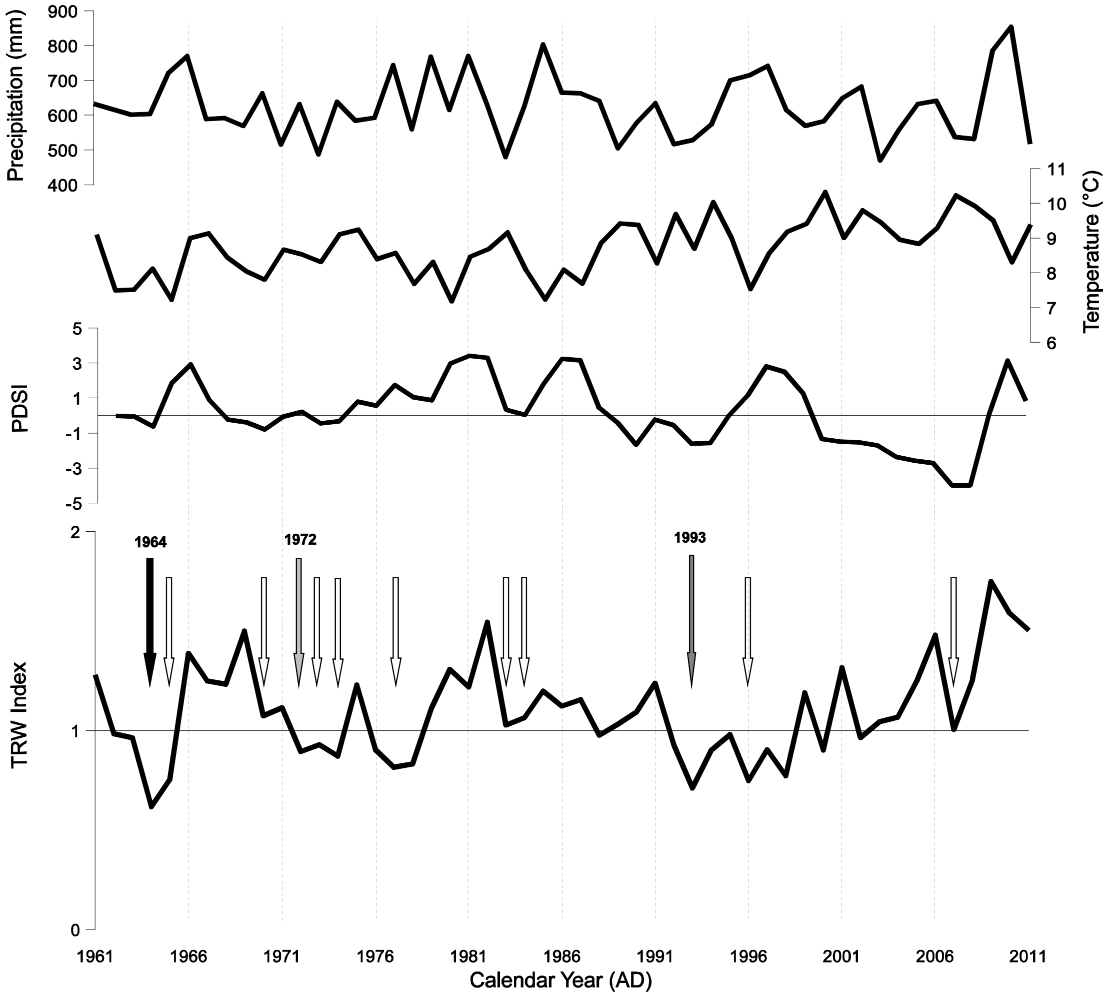

Fig. 4. *Comparison of precipitation, temperature and scPDSI (1961–2011) against oak growth (residual tree-ring index chronology), with negative pointer years highlighted additionally.*

Table 4. *Negative pointer years and abnormal climatic characteristics that might be relevant to interpretation (Year, 20–40% of trees sampled; Year, 40–60% of trees sampled; Year, 60–80% of trees sampled; Year, 80–100% of trees sampled).*

Negative pointer year	Abnormal climatic characteristics
1964	Very low precipitation (97 mm, average = 185 mm) and below average temperature (frost) from December 1963 to April 1964, above average temperature in June and July, and very low precipitation in August (15 mm).
1965	High precipitation (320 mm) and below average temperature from May to July.
1970	Very low precipitation from September to October 1969 (15 mm), and very low precipitation in May (16 mm).
1972	Above average precipitation in April and July, and above average temperature in December 1971, February and March.
1973	Very low precipitation in March (16 mm), and below average precipitation in May and August
1974	Low precipitation from February to April (50 mm, average = 109 mm), and above average temperature in March.
1977	Below average precipitation in May and June.
1983	Very low precipitation from July to August (49 mm, average = 157 mm), and hot July.
1984	Below average precipitation from October to December 1983, and low precipitation in June.
1993	Below average precipitation and hot summer in 1992, low precipitation from January to May (109 mm, average = 214 mm), and above average temperature in May.
1996	Below average temperature from December 1995 to March 1996.
2007	Very low precipitation from April to May (33 mm, average = 109 mm, April less than 1 mm), above average temperature from January to August, and low precipitation in August.

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Table 5. *Mean values of the main parameters of crown condition assessment. Parts of the crown: A — from the top to the first branching of at least 2nd order, B — from the first branching of at least 2nd order to the last branching of 1st-order branches, C — from the last branching of 1st-order branches to the bottommost branch in the stem.*

Title of plot	Defoliation			Total defoliation (A+B)	% of dead branches			Window (in A+B)			Secondary shoots (%)			Discoloration (%)	Proportion of reduced leaves (% in A+B)	Flowering	Fruiting
	Part of crown A	Part of crown B	Part of crown C		Part of crown A	Part of crown B	Part of crown C	Small	Middle	Big	Part of crown A	Part of crown B	Part of crown C				
1	33.3	48.5	41.8	48.3	13.5	22.3	26.4	12.0	21.5	14.3	0.0	45.5	100.0	0.0	0.0	0.0	0.0
2	52.0	53.0	35.0	53.0	20.5	17.5	7.6	16.5	23.5	13.0	0.0	51.5	100.0	0.0	0.0	0.0	0.0
3	53.0	60.8	45.0	59.5	16.4	22.0	10.0	16.8	22.0	20.5	0.0	55.5	100.0	0.0	0.0	0.0	0.0
TOTAL	**46.1**	**54.0**	**40.3**	**54.0**	**17.0**	**21.0**	**13.0**	**15.0**	**22.0**	**16.0**	**0.0**	**49.0**	**100.0**	**0.0**	**0.0**	**0.0**	**0.0**

found small, medium, and large windows (with secondary shoots), and their proportions were relatively balanced. Two trees had dry tops. The percentage of secondary shoots in the central part of the crown (B) exceeded 35% in all trees and was 49% on average; in the bottom part (C), there were only secondary shoots, and the majority were over one year old.

The relationship between the width of the last tree ring and the relative crown height, *i.e.*, % of crown height within the tree height, is presented in **Fig. 5**; the tree-ring width grows with the relative crown height. The effect of the percentage of secondary shoots in the central part of the crown (B) on the mean tree-ring width in the last ten years is presented in **Fig. 5**; the tree-ring width decreases with the percentage of secondary shoots. Secondary shoots were produced repeatedly in the last decade, as the secondary structure of the crown mostly consists of branches aged up to ten years, and the secondary shoots grow mainly on these branches.

Tortrix viridiana L. fed on all 60 trees, while *Loranthus europaeus* Jacg. was only present on two trees. No other biotic factors were found. One tree had stem damage in the form of small wounds. No changes in leaf color, leaf area reductions or shoot shortening were found. Fruiting was not recorded either; however, based on the number of fallen acorns, 2011 was a strong seeding year in the stands.

4. DISCUSSION

Sessile oak stores carbohydrates during autumn and uses them for spring growth. Earlywood begins forming approximately three weeks before bud break (Bergès *et al.*, 2008). In the period before bud break, a significant part of the stem increment has already been formed: Barbaroux and Bréda (2002) estimate 30%, while Bréda and Granier (1996) estimate 43%, but the latter study included not only earlywood, but also part of latewood. The spring mobilization of carbohydrates is likely to also be related to the conducting elements of oak as large tracheids are very sensitive to winter embolism. If a large part of earlywood tracheids from the previous year are embolized by winter frosts, the production of new tracheids is necessary, even before foliage, for spring renewal of the hydraulic conductivity. This ecophysiological model explains why earlywood growth in oak is generally less sensitive to exogenous factors, such as climatic factors, while latewood is much more sensitive (Bergès *et al.*, 2008; Michelot *et al.*, 2012). One promising indicator of the climatic effects on sites with mild humidity in which radial increment is not controlled by a limiting factor, at least in regard to earlywood, is not tree-ring width but, rather, tracheid width (Fonti and García-González, 2008). Because there is usually a major proportion of latewood in an oak ring, the responses of total tree-ring width and latewood are similar (Lebourgeois *et al.*, 2004).

The effect of autumn and winter climatic factors on the formation of carbohydrate storage has been proven repeatedly (Lebourgeois *et al.*, 2004; Cedro, 2007; Doležal *et al.*, 2010; Petráš and Mecko, 2011; Michelot *et al.,* 2012). In the area we studied, we mainly found an effect of the January climate: negative correlations were found for temperatures (mean, maximum, and minimum) and vapor pressure deficit; positive correlations were found for relative moisture and relative saturation of the soil profile in the top 40 cm. A high negative correlation between low temperatures in January and radial growth, measured by tree-ring width or earlywood growth, of sessile oak was also recorded in France (Becker *et al.*, 1994; Lebourgeois *et al.*, 2004; Michelot *et al.*, 2012).

The effects of the climate characteristics of the previous growing season on tree-ring formation has been shown considerably fewer times than the effects of autumn and winter, and existing studies have so far reported influence of August temperatures and precipitation (Petráš and Mecko, 2011; Michelot *et al.*, 2012). We observed a response to the climatic characteristics of July of the previous year: negative correlations were found for

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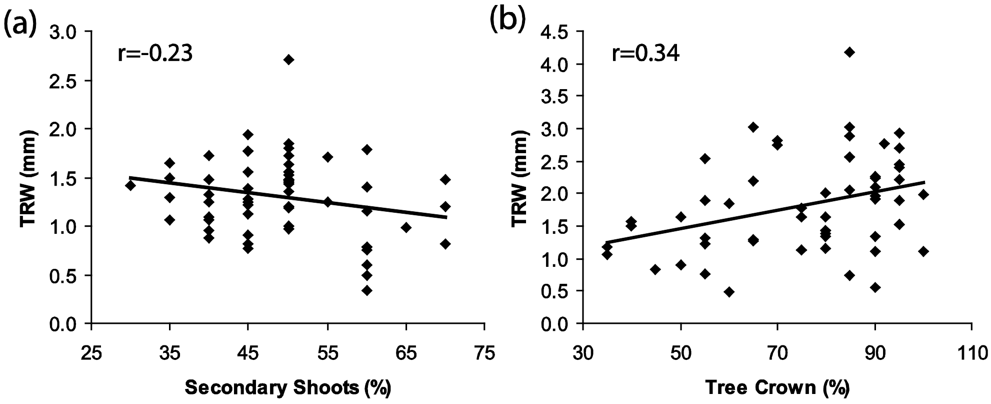

Fig. 5. *(a) Comparison of the proportion of secondary shoots with the mean tree-ring width in the last ten years, and (b) comparison of the relative crown height with the width of the last tree ring.*

temperatures (mean and maximum) and vapor pressure deficit; positive correlations were found for relative humidity, month SPI and SPEI.

When the tree ring is being formed, the effects of temperatures, precipitation and related characteristics in the growing season are limiting mainly during the period of oak latewood formation. In the study area of the Drahany Highlands, the effects of the studied characteristics were dominant in May (precipitation, SPI, SPEI) and June (precipitation, vapor pressure deficit, relative humidity, SPI, SPEI, ZIND, relative saturation of soil profile in the top 40 cm). Some of the characteristics also manifested significant correlations in July, August, and September (**Table 3**). The significant positive effect of precipitation in May and June has also been proven by a number of European dendroclimatological and xylogenetic studies dealing with the sessile oak in France (Becker *et al.*, 1994; Lebourgeois *et al.*, 2004; Mérian *et al.*, 2011; Michelot *et al.*, 2012), Romania (Popa *et al.*, 2013), Germany (Friedrichs *et al.*, 2009), Slovakia (Petráš and Mecko, 2011), Poland (Cedro, 2007; Bronisz *et al.*, 2012), and Moravia, Czech Republic (Doležal *et al.*, 2010). The negative effect of June (or July) temperatures has also been demonstrated repeatedly (Doležal *et al.*, 2010; Mérian *et al.*, 2011; Petráš and Mecko, 2011; Michelot *et al.*, 2012).

All of the established negative pointer years have some explanation in the extreme values of climatic factors accounting for the low increments (**Table 4**); most often, these were higher temperatures or lower precipitation during the growing season, mainly in the summer of the given year over individual months or longer periods for eight of the fourteen negative pointer years. Furthermore, for six negative pointer years, there was an unusual type of weather in the autumn and/or winter before the growing season in which the ring was formed. Some of the negative pointer years established in this study correspond to years that were established as negative pointer years in other regions and countries: 1964 (Becker *et al.*, 1994) in France, 1970 (Doležal *et al.*, 2010) in the Czech Republic, 1972 (Becker *et al.*, 1994) in France, 1983 (Becker *et al.*, 1994; Doležal *et al.*, 2010) in France and the Czech Republic, 1993 (Doležal *et al.*, 2010) in the Czech Republic, and 1996 (Lebourgeois *et al.*, 2004; Cedro, 2007) in France and Poland.

In 2009, a dendroclimatological study of the Norway spruce (*Picea abies*) was performed in the Drahany Highlands at a higher altitude, approximately 500 m a.s.l., on a site that was approximately 6 km from the four stands explored in this study (Rybníček *et al.*, 2012). In the case of spruce, the radial increment was most significantly affected by the climate in the summer of the year of ring formation; statistically significant correlations were found for precipitation (positive) and temperatures (negative) in May, June, July, and August. As for oak, spruce growth had a significant negative correlation with temperature in July of the previous year. In addition, temperatures in August and September (negative correlations), October of the previous year (positive correlation) and precipitation in September of the previous year (positive correlation) were significant.

The results of the crown condition can be compared with data from the ICP Forest network monitoring. Our results show a considerably higher defoliation of oak than average in the Czech Republic and Europe during the past ten years (ICP Forests data), which was approximately 30%. We suppose that the high level of defoliation was caused by drought in the area during previous years (see **Fig. 4**, low precipitation and PDSI in 2007–2008 and 2011). Defoliation was also partially caused by *Tortrix viridiana* L. larvae. According to forestry records, *Tortrix viridiana* larvae were also present in the stand in 2011, but their occurrence was low and did not cause any visible defoliation of the crowns. Increased abundance of *Tortrix viridiana* was also found in the first half of the 1990s; however, the caterpillars caused only low amounts

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of defoliation. The defoliation of oaks due to caterpillars may lead to a reduction in radial growth (Fajvan *et al.*, 2008); however, we suppose that the effect of caterpillar feeding on this stand was not significant because the abundance of *Tortrix* was only slightly increased. The stress load of past years is reflected in the presence of dry branches in the central part of the crowns of all of the trees examined. Additionally, there was a high proportion of secondary shoots: nearly half of all shoots in the central main part of the crown and all shoots in the bottom part were secondary shoots, and a majority of the shoots were over one year old. Restoration processes in the crown help to maintain or even increase crown height and radial growth if they are successful (**Fig. 5**). The effect of crown size has been repeatedly proven in literature (Assmann, 1970; Spiecker, 1991; Drobyshev *et al.*, 2007, *etc.*). However, repeated replacement of damaged shoots and branches is a very demanding process for trees that occurs at the expense of radial growth (**Fig. 5**) and results in a higher risk of tree adaptation capacity depletion and permanent damage or death (Lichtenthaler, 2006). The high rate of assimilatory tissue replacement supports the presence of a long-term stressor that lasted longer than the feeding of *Tortrix viridiana* larvae in 2011 and 2012. Considering the results of the dendroclimatological research, we can assume that climate stressors, especially the spells of summer drought, caused a great share of this stress. The reparation processes in progress manifest the unexhausted adaptation potential of the trees that allows for the replacement of damaged shoots.

5. CONCLUSIONS

In conclusion, we have found a close relationship between the climatic parameters of the environment, the tree-ring width and the assessed parameters of the tree crown. The wide range of climatic indices used in this study enabled us to assess the effects of temperatures and precipitation as well as soil humidity, water vapor pressure, solar radiation, and drought indices. We were able to find a satisfying explanation for most of the negative pointer years, which was mostly constituted by extreme values of climatic parameters. The results of this study were compared with the results of a dendroclimatic study of spruce conducted on a plot 6 km away in 2009; the 2009 study independently supports some of our findings. The defoliation found was higher than the mean values for the sessile oak and the pedunculate oak in Europe (based on ICP Forest data) in the last ten years. We ascertained that the repeated restoration processes occurring in the crown in response to permanent stress have a negative effect on radial growth during the period when secondary shoots are produced. Our results can be generalized not only for the thirteen highly similar natural forest areas in the Czech Republic but also other analogous areas in central Europe. Tree-ring series were added to the oak tree-ring chronology for the Czech Republic, improving its replication for the last 150 years.

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