

Different drought sensitivity traits of young sessile oak (*Quercus petraea* (Matt.) Liebl.) and Turkey oak (*Quercus cerris* L.) stands along a precipitation gradient in Hungary

Norbert Mórincz^{a,*}, Gábor Illés^a, Ilona Mészáros^b, Balázs Garamszegi^a, Imre Berki^c, Zsófia Bakacsi^d, József Kámpel^a, Orsolya Szabó^a, Ervin Rasztovits^e, Klára Cseke^f, Katalin Bereczki^a, Tamás Márton Németh^a

^a Department of Ecology and Forest Management, NARIC Forest Research Institute, Hungary¹

^b Department of Botany, Faculty of Science and Technology, University of Debrecen, Hungary

^c Faculty of Forestry, University of Sopron, Hungary

^d Institute for Soil Sciences, Centre for Agricultural Research, Hungary

^e Unaffiliated Researcher

^f Department of Tree Breeding, NARIC Forest Research Institute, Hungary¹

ARTICLE INFO

Keywords:

Drought
Growth response
Quercus petraea
Quercus cerris
Tree rings
Water stress index

ABSTRACT

This paper analyses the drought-induced growth responses of two ecologically and economically important broadleaf tree species, namely sessile oak (*Quercus petraea* (Matt.) Liebl.) and Turkey oak (*Quercus cerris* L.) in south-western Hungary. Although both have been described as drought-tolerant species, our understanding of their growth responses to drought extremes is still limited. Forest stands of younger ages of the target species were sampled along a precipitation gradient under similar soil conditions. 136 tree-ring samples were used to build six species- and site-specific chronologies. We also applied several dendroecological metrics to assess the drought sensitivity of the species. Water deficit was estimated by various drought indices including the soil water-budget based water stress index. The results indicated a strong dependency of annual tree-ring width of both species on the water availability of summer months in the actual year of ring formation. However, we found markedly different reaction of the two species against drought conditions. Turkey oak responded more sensitively to droughts than sessile oak revealed by the significantly lower resistance and higher recovery potential of this species. The more plastic behaviour of Turkey oak could be also perceived by the higher sensitivity of its tree-ring chronologies and by the observed relationship between resistance and recovery that showed a closer fit to the line of full resilience in case of this species. Regarding the precipitation gradient, a linearly proportional increase of growth reduction with rising water stress was found for Turkey oak while the growth response of sessile oak decreased considerably with increasing aridity indicating lower growth plasticity of sessile oak to droughts there. Based on our findings it seems that Turkey oak copes better with droughts than sessile oak and may gain competitive advantages under the projected climate change in Hungary.

1. Introduction

Droughts occurred with increasing frequency and severity in Europe over the last decades (Mishra and Singh, 2010; Spinoni et al., 2015) and this trend is expected to continue in the future (IPCC, 2018). One of its effects is decreased stand growth, which could negatively impact forest productivity (Bertini et al., 2011; Peltier et al., 2016; Camarero et al.,

2018; Mátyás et al., 2018; Brodribb et al., 2020; Schuldt et al., 2020). Moreover, frequent, prolonged and extreme droughts are often key drivers of widespread mass mortality of forest trees either directly or through secondary biotic agents (Gustafson and Sturtevant, 2013; Williams et al., 2013; Rasztovits et al., 2014; Busotti and Pollastrini, 2017). While such processes are often presumed to be more intensive along the xeric limit of tree species distribution (Giuggiola et al., 2010; Weber

* Corresponding author at: University of Sopron, Forest Research Institute, Bajcsy-Zsilinszky utca 4, 9400 Sopron, Hungary.

E-mail address: morinczn@erti.hu (N. Mórincz).

¹ Current affiliation: University of Sopron, Forest Research Institute, Hungary.

et al., 2013) include widespread tree mortality, the drought-driven decrease of tree growth may be equally important in the core distribution areas of the species, as well (Cavin and Jump, 2017).

In general, knowledge on the response of important tree species native to temperate regions of Europe (e.g. European beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.) to drought is progressing (Scharnweber et al., 2011; Weber et al., 2013; Zimmermann et al., 2015; Kolár et al., 2017; Árvai et al., 2018; Kunz et al., 2018). Nevertheless, only a few climate-tree vitality studies have included species that are assumed to be more drought-tolerant in Central Europe such as Turkey oak (*Quercus cerris* L.), Scots pine (*Pinus sylvestris* L.) or Black pine (*Pinus nigra* Arn.) (Mészáros et al., 2011; Misi and Náfrádi, 2017; Mórincz et al., 2018; Stojanović et al., 2018).

In Hungary, sessile oak and Turkey oak are both ecologically and also economically among the most important tree species, covering 20.9% of the total forested area (National Forestry Database, 2010). As long-living dominant species in their corresponding habitats, both of them have both mid-successional and late-successional species characteristics since they are light-demanding and have deep penetrating roots and can produce large reserves of acorns, respectively. They grow on light and well-drained, often rocky soils found on hills and mountains and tolerate low soil pH. Both species are considered to be drought tolerant across Europe (Nardini et al., 1999; Härdtle et al., 2013; Zimmermann et al., 2015). Due to projected unfavourable climatic changes, Turkey oak is, moreover, considered to be a suitable potential substitute species of sessile oak in several forest sites of Hungary (Führer et al., 2011).

In Hungary, the vitality of oak forests (especially sessile and pedunculate oak – *Quercus robur* L.) has already shown significant decline owing to the prolonged drought periods in the 1980s (Jakucs et al., 1986) as one of a precursor event to the series of extremely dry years since the beginning of the 1990s (Mészáros et al., 2008, 2011; Árvai et al., 2018; Gulyás et al., 2019).

Few studies compared the ecophysiological reaction of Turkey oak and sessile oak to drought conditions (Cutini, 1997; Mészáros et al., 2011) and also few dendroclimatological comparisons of these species are existing so far (Brêteau-Amores, 2018). As more extreme and prolonged droughts are expected due to climate change, it becomes particularly important how the growth of Turkey oak responds to drought conditions compared to sessile oak. Moreover, younger trees have been investigated rarely in their response to drought, albeit it is an important question when predicting the future competitive strength of the tree species (Günthardt-Goerg et al., 2013; Gulyás et al., 2019).

In this study first, we compared the climate - tree growth relationship of younger sessile and Turkey oak trees along a precipitation gradient using dendrochronological data and climatic indices. Growth responses to droughts were analysed using several dendroecological metrics in concert that may provide a more comprehensive understanding of drought responses. We compared the 'Lloret indices' (Lloret et al., 2011) complemented with two other indices proposed by Thurm et al. (2016) and also used a recently proposed approach employing the 'line of full resilience' (Schwarz et al., 2020) as a reference for the analysed species.

2. Materials and methods

2.1. Study sites

The three study sites are located in Somogy County, south-western Hungary, near to the municipalities (in parentheses the respective site codes) of Iharos (IHA), Zselic (ZSE), Szántód (SZA) and situated in elevations ranging between 210 and 290 m above sea level. The precipitation gradient describes a difference in mean annual precipitation (for the period 1985–2018) between the most humid (IHA: 774 mm; denoting the 70th and 95th percentiles of the annual precipitation considering the distribution of sessile and Turkey oak in Hungary, respectively) and the most arid (SZA: 614 mm; 27th and 35th percentiles of the annual precipitation for the species, respectively) sites of 160 mm.

Additionally, an intermediate location (ZSE: 711 mm; 55th and 75th percentiles for the species, respectively) was included.

In two of the sites (IHA and SZA), one younger mixed stand of sessile (*Quercus petraea*; hereafter QP) and Turkey oak (*Quercus cerris*; hereafter QC) was designated for data collection. In the site ZSE the selected mixed stands are situated in different forest subcompartments but close (distance < 500 m) to each other (Table 1). In the mixed stands, there are several other minor species such as European hornbeam (*Carpinus betulus*), Larch (*Larix decidua*) and Silver Linden (*Tilia tomentosa* Moench). For the sake of comparison, all stands are located in zonal situation on similar in-site conditions of deep loamy brown forest soil with low rock fraction content and no surplus water. Sampled trees were selected exclusively from the highest, and (co-)dominant crown layer to exclude stand structure effects. All trees have been grown from seed.

2.2. Meteorological data and soil water budget calculations

Temporal change of temperature showed a clear warming trend during the last three decades in south-western Hungary. The difference in annual precipitation among the study sites reduced due to the slight decrease of precipitation in the humid site IHA and the observed increase in the other two sites ZSE and SZA during the analysed period (Fig. 2).

To analyse the growth-climate response, meteorological data were obtained from different sources for the period 1985–2018.

Daily minimum and maximum air temperatures were acquired from the DAYMET database (Moreno and Hasenauer, 2015) of 1 km resolution from 1985 to 2017 that is a downscaled and improved data set based on the 30x30 km resolution E-OBS climate database (Haylock et al., 2008). We selected the DAYMET database because it has high spatial resolution thus the elevation-dependent temperature is well represented even with scarce input station data from Hungary. For the year 2018, we used the measured temperature data of the nearest (distance < 15 km) meteorological stations (Nagykanizsa, Kaposvár, Siófok) of the Hungarian Meteorological Service adjusted to the elevation of the sites using monthly elevation gradient (Pécze, 1979) (Fig. 1). Daily minimum and maximum temperatures were averaged to mean daily temperature and subsequently to monthly values.

Monthly precipitation data was gathered from the homogenized CARPATCLIM database (Szalai et al., 2013) of ~ 10 km resolution from 1985 to 2010. The CARPATCLIM database was created by a high number of station data therefore the spatial variability of precipitation is well represented. We also used the precipitation data of the nearest meteorological stations operated by the Hungarian Meteorological Service for the period 2011–2018 (Fig. 1).

We derived climate indices from monthly meteorological data for correlation with growth at different time scales (annual/seasonal/monthly) with particular attention to water availability. The multiscalar Standardized Precipitation Evapotranspiration Index (SPEI; Vicente-Serrano et al., 2010) was calculated on monthly mean temperature and precipitation sums using the R package SPEI (Beguería et al., 2014). The Forestry Aridity Index (FAI; Führer et al., 2011) was defined as the ratio of the average temperature of July and August and the precipitation sums of May to July plus the precipitation sum from July to August corresponding to the main growth and organic matter production of forests.

For monthly water balance modelling, we used the Thornthwaite-type model (Thornthwaite, 1948) for the period 1985–2018. The input variables for the model were monthly mean air temperature, precipitation sum, the latitude of the sites and the soil–water storage capacity, defined as the water content difference between the field capacity ($pF = 2.5$) and permanent wilting point ($pF = 4.2$), multiplied by the vertical extent of the root zone. We set the rooting depth uniformly to 1 m in all stands by visual observation of fine roots in the soil pits. Soil samples were taken from three to four depths according to soil horizons in each site. Three repetitions of undisturbed soil samples for water retention

Table 1

Main site and stand characteristics (DBH: mean diameter at breast height).

Site	Location	Lat./Lon.	Species	Elevation (a.m. s.l.)	Slope (°) /aspect	Stand age in 2019 (years)	Mixing ratio of species stems (%)	Mean tree height (m)	DBH (cm)
IHA	Iharos	46.32 N/	QP	220	7.5/east	29	38	13	10.8
		17.06 E	QC	220	7.5/east	29	15	13	13.1
ZSE	Zselic	46.25 N/	QP	280	2/south-west	35	51	15	11.7
		17.75 E	QC	250	8/south-west	36	49	20	13.7
SZA	Szántód	46.83 N/	QP	225	5/west	33	13	15	15.9
		17.94 E	QC	225	5/west	33	67	16	13.9

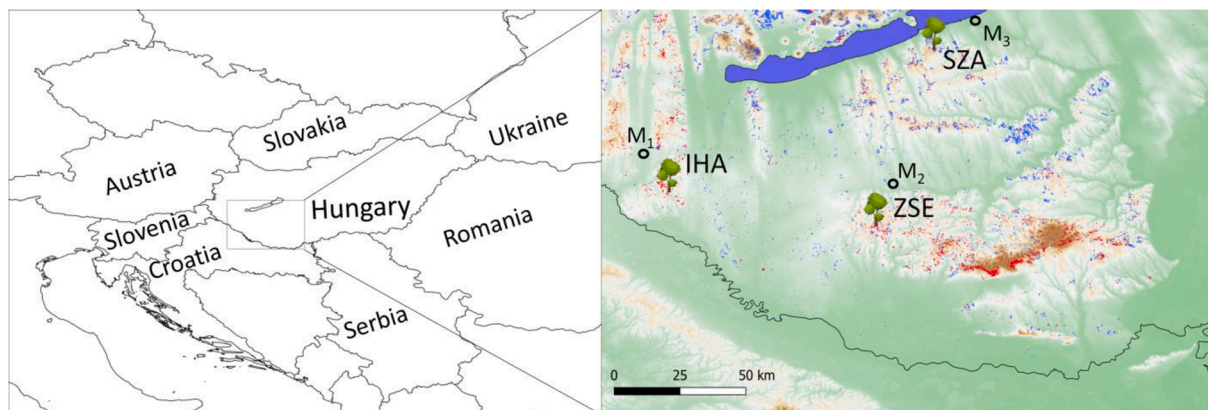


Fig. 1. Location of the three study sites (IHA, ZSE, SZA); M₁, M₂ and M₃ are the meteorological stations of Nagykanizsa, Kaposvár and Siófok, respectively; the dots mark the locations of sub-compartments where the mixture ratio of *Quercus petraea* (red) and *Quercus cerris* (blue) was the highest. (Source: National Forestry Database, 2010). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

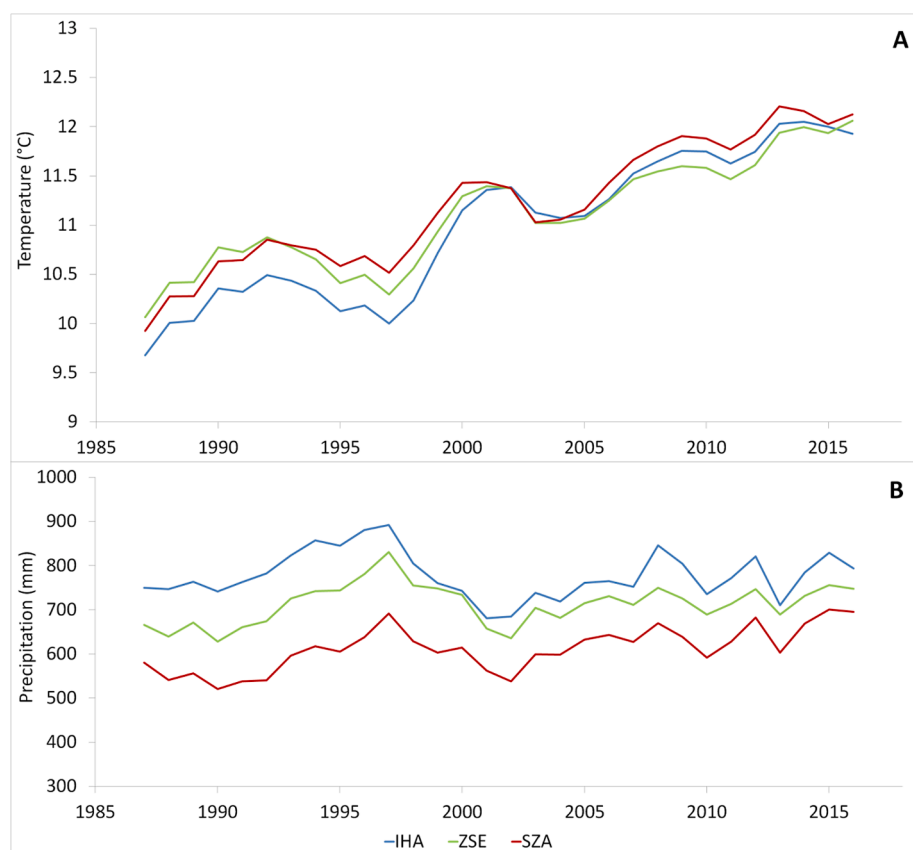


Fig. 2. Trends in annual mean temperature and precipitation sum of the three study sites (IHA, ZSE, SZA) for the period 1985–2018, curves are smoothed by 5 years moving average (Source: Hungarian Meteorological Service, CARPATCLIM database (Szalai et al., 2013), DAYMET database (Moreno and Hasenauer, 2015)).

were analysed at four different depths down to 1.3 m by cylinders of 100 cm³ (Table 2). We modified the Thornthwaite-type model by including precipitation interception of the younger stands as follows: Jan-Feb: 5% Mar: 10%, Apr: 15%, May-Sep: 20%, Oct: 15%, Nov: 10%, Dec: 5%. The monthly interception values represent our estimations based on seasonal leaf phenology as we lacked reference interception data for younger oak stands in Hungary. As an additional predictor variable in the growth-climate analysis, we used the water stress index of the summer months (I_s) calculated by dividing soil water deficit and the maximum extractable water for the 1st-meter soil depth described in Granier et al. (1999).

2.3. Core sampling and processing of tree-ring data

In each stand, 12 dominant trees per species were selected for sampling. Two increment cores were collected in N and E positions from each sample tree (in total 144 cores) at breast height (1.3 m) using a Pressler increment borer (Haglöf, Långsele, Sweden). Cores were stored in plastic straws, air-dried, then were glued to grooved wooden mounting boards. Cores were sanded and scanned with high-resolution (1200 dpi). Tree-ring widths (TRW) were measured on digital images to 0.001 mm using WinDENDRO software ver. 2014a (Regent Instruments Canada Inc. 2014). Cross-dating was checked by COFECHA (Holmes, 1983). All cores with potential errors were rechecked and corrected if it was possible. Otherwise, they were omitted from further investigations that left a total of 136 cores to be considered for further analysis.

Detrending of tree-ring width series and building of the species-specific chronologies for each site were performed based on the arithmetic means of the two cores per individual stems and by using the facilities of the 'dplR' package under the R statistical program (Bunn, 2008; R Core Team, 2013).

A smoothing spline method with the initial settings of 50% frequency response at a wavelength of 67% of each series length was found to well remove any age-related trends due to the relatively short series. Detrended series were also checked by the Akaike information criterion (AIC) which suggested no need for further processing and use of pre-whitened data, despite the elsewhere reported higher autocorrelation in tree-ring series of oaks (van der Werf et al., 2007; Kern et al., 2013). Ring-width index chronologies were built as the bi-weight robust mean of individual series, where sample depth along the time series reached or exceeded a minimum of five individual stems. The signal strength of the final index chronologies was checked by the expressed population signal (EPS) and mean inter-series correlation (R_{bar}) (Table 3). EPS was determined on a 30-year running window with an overlap of 10 years for each tree-ring series to assess the signal strength of the chronologies (Briffa et al., 1983; Wigley et al., 1984).

Following prior knowledge on reported large-scale pest outbreaks in the region (Hirka, 2006), we investigated the biotic effect on radial growth applying Cook's distance to the linear regression between radial growth and water stress index to decide if there were outliers in the datasets (Cook and Weisberg, 1982). Applying the same methods, we studied the relationship between the summer mean of the standardized NDVI from the MODIS satellite imagery (Somogyi et al., 2018) and the

water stress index to confirm that the outlier years were affected by biotic damages, indicated by below normal photosynthetic activity. Additionally, we analysed if the biotic effect on radial growth of the species could be detected in the next year using the relationship between radial growth and the water stress index. In this way, we could select the years affected by biotic damages that were omitted from further processing.

2.4. Data analysis

Pearson's correlation coefficients were calculated between the species and site-specific standard chronologies and monthly and seasonal meteorological data (mean temperature and precipitation sum) and derived indices (FAI, SPEI and I_s). Monthly correlation coefficients were calculated using an 18-month time period from April of the previous year to September of the actual year of ring formation, considering that weather of the previous year affects growth during the following year. Additionally, we computed the SPEI at 2–12 months long scales to allow quantifying the effects of meteorological conditions on radial growth at different time scales. A 15-year's moving window correlation analysis was applied to test for the temporal stability of the relationship of meteorological variable showing the highest correlation to the annual tree ring width. The correlation of the selected variables with the radial growth of the oak species was compared and tested for significance using the method by Diedenhofen and Musch (2015).

To evaluate the reaction of the species to changing climatic conditions, we selected the period of 2001–2018 where tree-ring data was available for all stands. The meteorological index with the highest correlation to radial growth was compared with the corresponding tree-ring values using a non-parametric local regression approach for all stands due to the non-linear nature of the relationships.

We comparatively analysed the growth response to drought years for the oak species located on sites with different climatic conditions. Drought years were determined by the standardized summer water stress index. The standardization was done by subtracting the mean of the absolute values from the given absolute value and dividing by the standard deviation of the absolute values. Years were considered drought years when they deviated more than one half standard deviations from the long-term mean (time period: 1985–2018).

For the drought years or multi-year drought periods, three indices of drought reaction were calculated following Lloret et al. (2011). These indices describe how the trees can withstand drought (resistance), restore from drops during the drought (recovery), the capacity to reach pre-drought growth levels (resilience). We used one year of growth to represent the pre-and post-drought growth levels to have as much drought events as possible without the intersection of the periods of the frequently occurring droughts. For multi-year droughts, the resistance and recovery indices were calculated by averaging the radial growth of successive drought years.

Additionally, two more indices were used – length of the recovery period (RP) and total growth reduction (TGR) – based on Thurm et al. (2016). RP means the time (unit is year) required to reach the pre-drought mean growth level again inclusive the drought years. TGR describes the sum of growth reduction due to the drought, including drought year and the loss of growth during RP. We used here the mean value of the detrended chronologies (unity) as the pre-drought growth level, representing "normal" growth to eliminate the effect of unusual growth in the pre-drought years. The indices were calculated from the detrended radial growth since raw data is usually strongly affected by natural age-related growth trends and variations in tree dimension (Lloret et al., 2011). We computed the sum of TGR for all drought events per species considering all stands of the sites. To evaluate the differences among the sites and species we used the ratio of TGR and the I_s for all available drought years.

Finally, we compared regression fits for the relationship between recovery and resistance for all available drought events with the

Table 2

Main soil characteristic of the sites. Water content at pF 2,5 and 4,2 and pH (H₂O) data are means of all sampled soil layers.

Site	IHA	ZSE		SZA
Stand	QC-QP	QC	QP	QC-QP
Maximum available soil water content (mm/m)	157	176	166	157
Water content at pF 2,5 (mm)	33.88	32.4	32.7	32.33
Water content at pF 4,2 (mm)	17.65	13.9	14.4	14.93
pH (H ₂ O)	5.16	6.17	5.99	5.72

Table 3

Summary information of tree ring data and chronologies (MSL: mean segment length, MRW: mean ring width (and its standard deviation), MS: mean sensitivity, FDY: first dated ring, LDY: last dated ring, Rbar: mean inter-series correlation, EPS: expressed population signal).

Site	Species	Raw data			Detrended chronology				
		MSL (years)	MRW (mm) (mm/year)	Std dev.	MS	FDY	LDY	Rbar	EPS
IHA	QP	17	3.23	1.35	0.24	2000	2019	0.703	0.965
IHA	QC	18	3.59	1.42	0.32	1999	2019	0.806	0.979
ZSE	QP	26	2.47	1.27	0.22	1989	2019	0.532	0.925
ZSE	QC	26	2.60	1.12	0.29	1989	2019	0.477	0.912
SZA	QP	24	3.38	1.68	0.28	1992	2019	0.551	0.933
SZA	QC	24	2.85	1.35	0.42	1990	2019	0.806	0.980

theoretical line of full resilience to further facilitate the understanding of drought tolerance of the species (Schwarz et al., 2020).

3. Results and discussions

3.1. Tree-ring chronology statistics

The length of individual growth series varied from 14 to 30 years (Table 3). For the study period the mean values of EPS were between 0.91 and 0.98, thus exceeded a more rigorous threshold of 0.9 (Mérian et al., 2013), and thus demonstrating a representative sampling in the study areas and populations. The mean ring width (MRW) did not differ significantly between the species, yet it was slightly greater for QP in site SZA and QC in sites IHA and ZSE. The differences in mean site-specific MRW of both species between the site ZSE and the other sites were significant with $p < 0.001$. Cross-dating resulted in a mean inter-chronology correlation of 0.65 of the detrended series and the site-specific individual series showed also high similarity, in the range of $r = 0.59$ – 0.87 . We found, however, that the individual growth series of the chronologies were less similar in the first years as expected from the juvenile growth of trees.

Juvenile growth of trees may influence the reliability of the resultant tree-ring chronologies by its higher and irregular growth rates (Speer, 2010). Considering the age of trees based on available stand-level inventory data and the year of the first dated rings of the chronologies, the starting age of trees ranged between 5 and 10 years in our analysis. Nevertheless, the overall high intra-chronology Rbar statistics suggested a common climatic forcing throughout the chronologies leading to similar variance, likely due to the relatively short series representing tree growth at their age of high growing vigour and variability following the early juvenile growth stage (Table 3).

Mean sensitivity was generally higher for QC and showed an increase from the humid to the more arid site for both species (QC: 0.29–0.42, QP: 0.22–0.28). The higher annual variance of QC chronologies compared to QP was also visible in Fig. 3.

Non-climate factors such as insect outbreaks might also affect the radial growth, through reduction of trees' photosynthetic capacity either due to foliage damages or by (complete) defoliation (Csóka and Hirka, 2009; Klapwijk et al., 2013), allowing these disturbances to be identified in tree ring chronologies. The year 2005 appeared as an outlier for both species in the site SZA, but interestingly not in the other two sites. Taken into account both the summer mean of the standardized NDVI and the water stress index, such preliminary comparisons also revealed that besides the year 2005, the year 2006 was also likely affected by biotic damages in line with the reported peak years of gypsy moth (*Lymantria dispar* L.) outbreak in these two years causing 45,000 ha damage in Somogy county (Hirka, 2006). The biotic effect on radial growth of sessile oak was also traceable in 2006 under favourable soil moisture conditions. Contrarily, Turkey oak seemed to be recovered completely in 2006 (Fig. 3).

Based on the former analysis we decided to omit the years 2005 and 2006 in the climate-growth analysis in the site SZA. Here, we did not use the drought year 2007 in the drought response analysis since it was

probably majorly influenced by the biotic damages beforehand.

3.2. Climate and tree-growth relationships

Correlation coefficients between climatic parameters and detrended ring-width index series were highest for both species for summer and spring of the actual year of ring formation (Fig. 4). Positive correlations with summer precipitation ($r = 0.45$ for both species) along with negative correlation of temperature (QC: $r = -0.49$ and QP: -0.46) identify current year summer water availability as the main controlling factor of tree growth for both species. The highest correlation (QC: $r = -0.68$ and QP: $r = -0.66$) was found for the water stress index of the actual summer (I_s) that takes into account the soil water storage capacities of the sites. The summer correlation coefficients of the SPEI (QC: $r = 0.45$ and QP: $r = 0.55$) and FAI (QC: $r = -0.49$ and QP: $r = -0.52$) were also statistically significant and the correlation coefficients did not differ significantly from each other (Diedenhofen and Musch, 2015).

Generally, the climatic condition of the previous year was less important for the radial growth of both species as mainly found in other studies with *Quercus* species (e.g. Vanhellemont et al., 2019). Nevertheless, we found a significant correlation between growth and the weather conditions of the previous autumn for both species. Contrarily to the expectations, the weather conditions of previous summer were in most of the cases inversely correlated to the radial growth (Fig. 4).

Regarding the precipitation gradient, we found no clear trend among the sites, but the most humid site IHA displayed the highest overall correlations ($r = 0.56$, 0.41 and 0.49 for IHA, ZSE and SZA sites, respectively) to the analysed climatic indices for the actual year. Interestingly, the correlation of summer temperature with growth showed a decreasing trend from the humid to the more arid site for both species.

Since the water stress index of summer had the highest correlation with tree growth, we used this variable as the climatic predictor during the subsequent analysis. The correlation analysis with a 15-year moving window revealed that the correlation of I_s with radial growth was stable for all stands with standard deviations between 0.03 and 0.08.

Several authors suggested that favourable soil water availability during summer induced the formation of wide rings and vice versa (Friedrichs et al., 2009; Scharnweber et al., 2011; Rybníček et al., 2016; Kovács and Czigány, 2017). The temperature showed significant negative correlations in June and partly in August of the current year being an important factor on summer moisture availability (Cufar et al., 2014). In general, the climate - tree growth relationships revealed by our study are comparable to those found for old stands of oaks in Germany (Friedrichs et al., 2009), in Slovenia (Cufar et al., 2014), in Czech Republic (Rybníček et al., 2016), in Romania (Nechita et al., 2017), in Serbia (Stojanović et al., 2018) and in Belgium (Vanhellemont et al., 2019) showing that oaks are particularly sensitive to climatic conditions in spring (but also for the months preceding the onset of ring formation) and in the early summer months.

Relationship between the detrended tree ring width index (scaled to zero for better interpretation) and the summer water stress index showed that the local regression lines were quite similar for the species in the same sites (Fig. 5). QC responded dynamically to the amount of

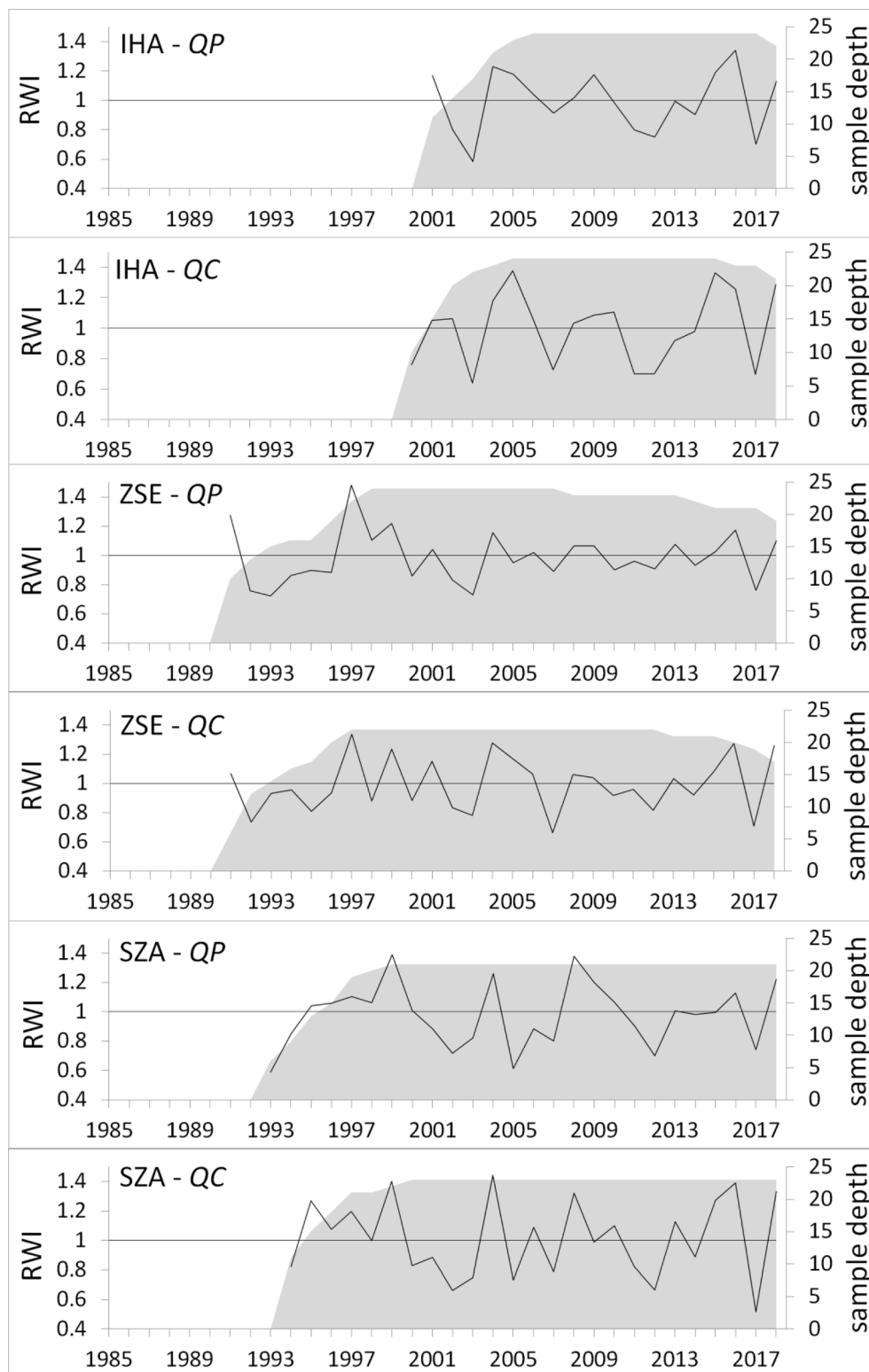


Fig. 3. Detrended chronologies (RWI) of the oak species of the study sites IHA, ZSE and SZA; in grey sample replication (series).

available soil water by reducing its growth during droughts and having high growth rates in favourable years. On the other hand, the growth of QP was less sensitive to the changing soil water conditions. The growth of QC was mainly above the growth of QP during slight water deficits ($I_s < 0.5$), but QC responded with greater growth reductions to more severe water shortages.

Regarding the precipitation gradient, we found that the relationship

between the radial growth and the summer water stress index was different in the sites (Fig. 5). Although the local regressions were similar in site IHA and SZA, the growth started to decline steeper at larger water deficits in site SZA. In site ZSE the radial growth of the species was less sensitive to the changing soil water availability, but there was only one particularly strong summer drought here.

The high adaptation potential of oak populations to local climatic

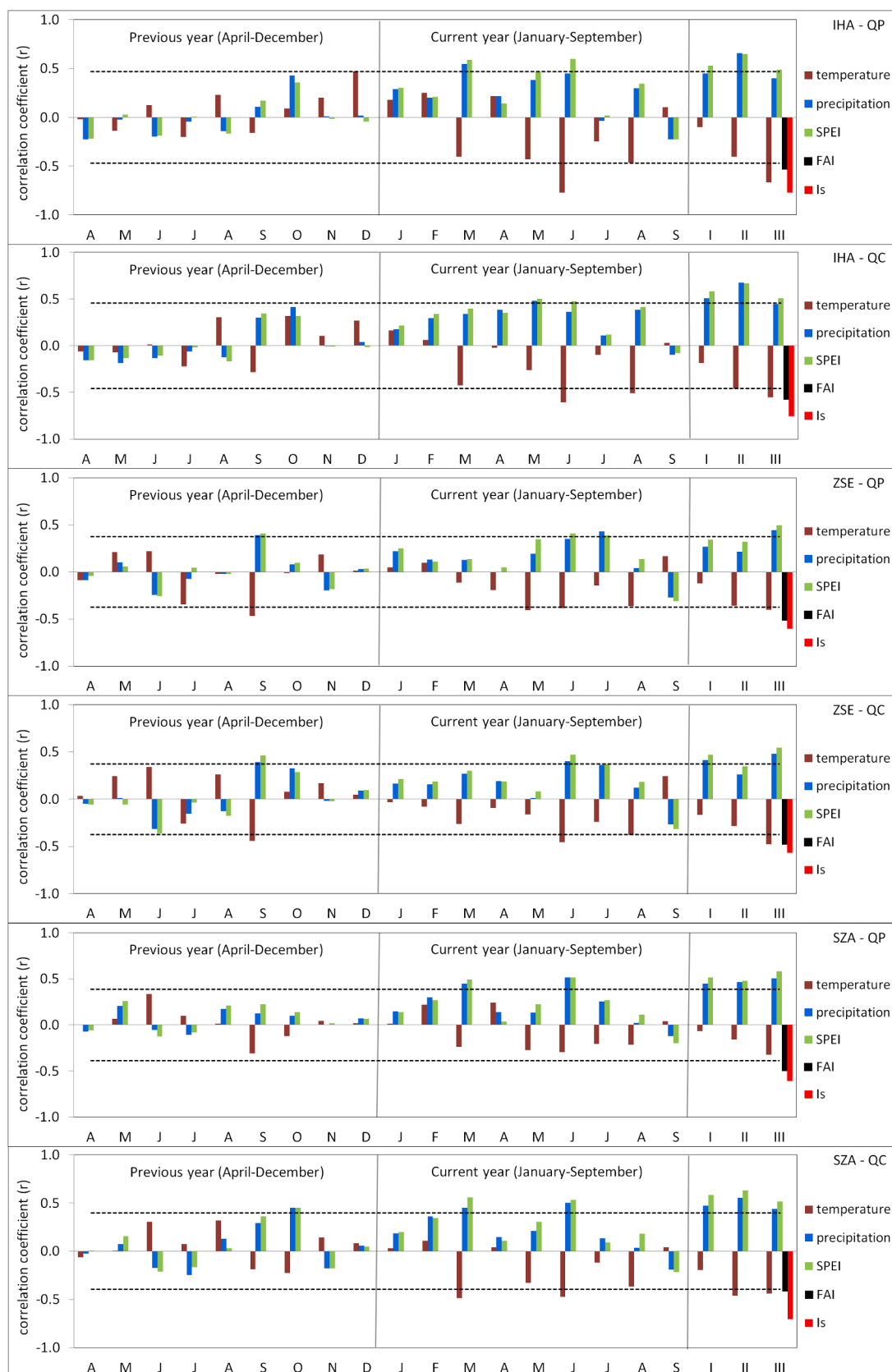


Fig. 4. Correlation coefficients between monthly and seasonal climate parameters and detrended chronologies of the oak stands. Dashed lines indicate the 95% significant level. Previous year: April–December, Current year: January–September, I: January–December, II: March–April–May, III: June–July–August (FAI: May–August).

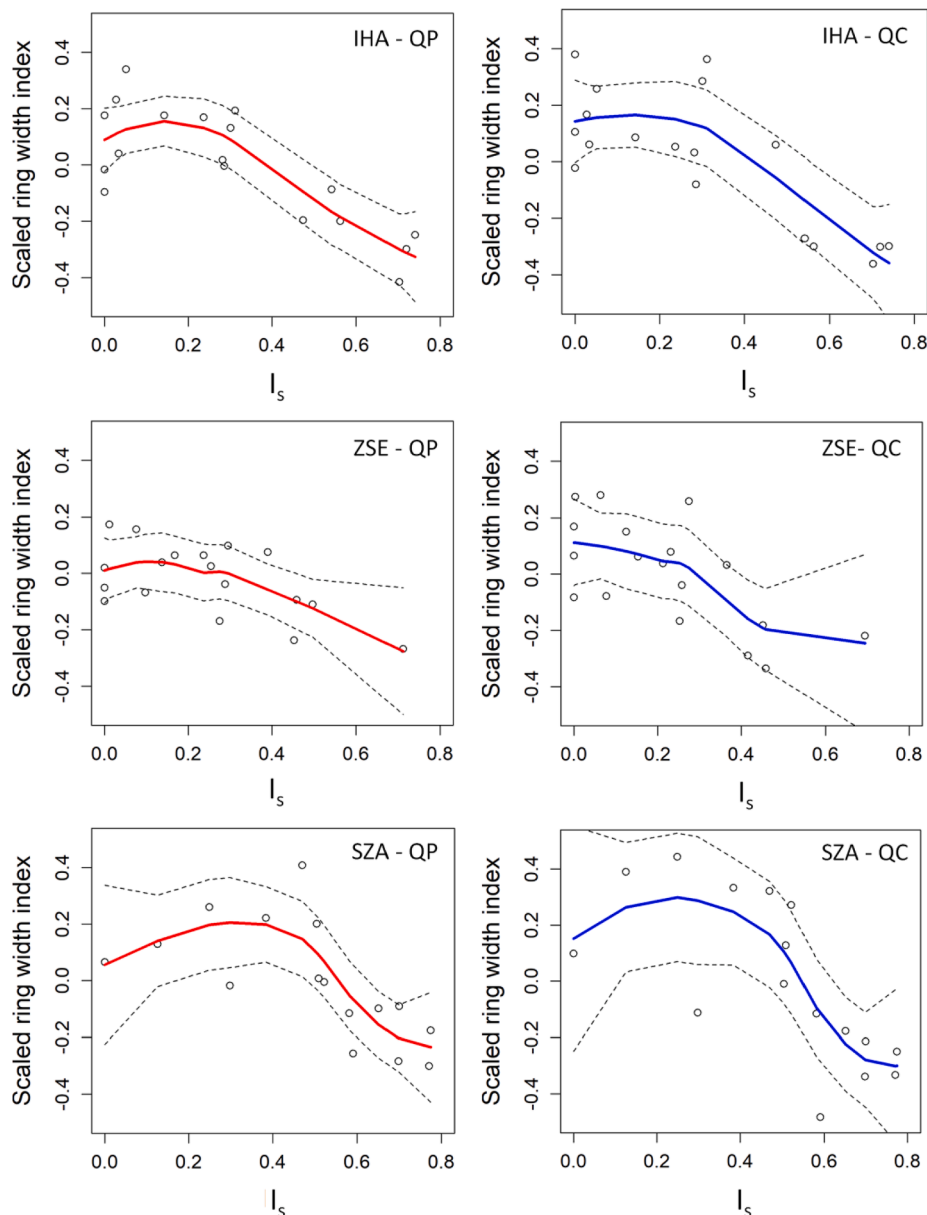


Fig. 5. The relationship between the detrended ring width series (scaled to zero; scaled RWI) and the annual values of summer water stress indices (I_s) for the sites IHA, ZSE and SZA for the period 2001–2018. Solid red and blue lines denote Loess regressions with a span value of 0.9 and dashed lines are the 97.5% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

factors is of particular interest since adaptive responses to environmental stress are to a large extent governed by genetic diversity (Gieger and Thomas, 2005; Clark et al., 2016). Therefore, phenotypic plasticity may interfere in our attempt to make simple generalisations regarding the effect of drought stress on populations under different environmental conditions.

3.3. Responses of radial growth to drought periods

We selected several drought periods ($n = 13$) by taking into account the available tree ring data of the sites and by considering subsequent drought years as multi-year drought periods (Fig. 6).

For calculation of the three Lloret indices (resistance, recovery and resilience) we used all available drought events (Fig. 6). The merged data of all stands and drought events showed that the resistance of QP was significantly higher than that of QC ($t = -1.95$, $p < 0.05$). Contrarily, the mean recovery of QC was significantly higher than for QP

($t = 3.03$, $p < 0.05$) and thus the resulting resilience was very similar (Fig. 7).

Several studies found a general pattern between resistance and recovery namely species with high resistance have a low capacity for recovery and vice versa (Hoffmann et al., 2018). These patterns denote different strategies (isohydric vs anisohydric) of the species to cope with droughts (Martínez-Vilalta et al., 2014; Gazol et al., 2017; Mirfenderesgi et al., 2019; Schwarz et al., 2020). Pretzsch et al. (2012a) found that sessile oak has strongly anisohydric character and high drought resistance but recovers slowly after drought events. The underlying physiological patterns may play an important role in response to soil water limitations (Tognetti et al., 1996; Levanič et al., 2011; Mészáros et al., 2011; Pretzsch et al., 2012a). QP probably keeps up transpiration during drought that may result in earlier depletion of available water while QC quickly closes their stomata during water shortage and so reduces transpiration and carbon acquisition. Yet, maintaining photosynthesis during drought may require trees to invest more carbohydrates that will

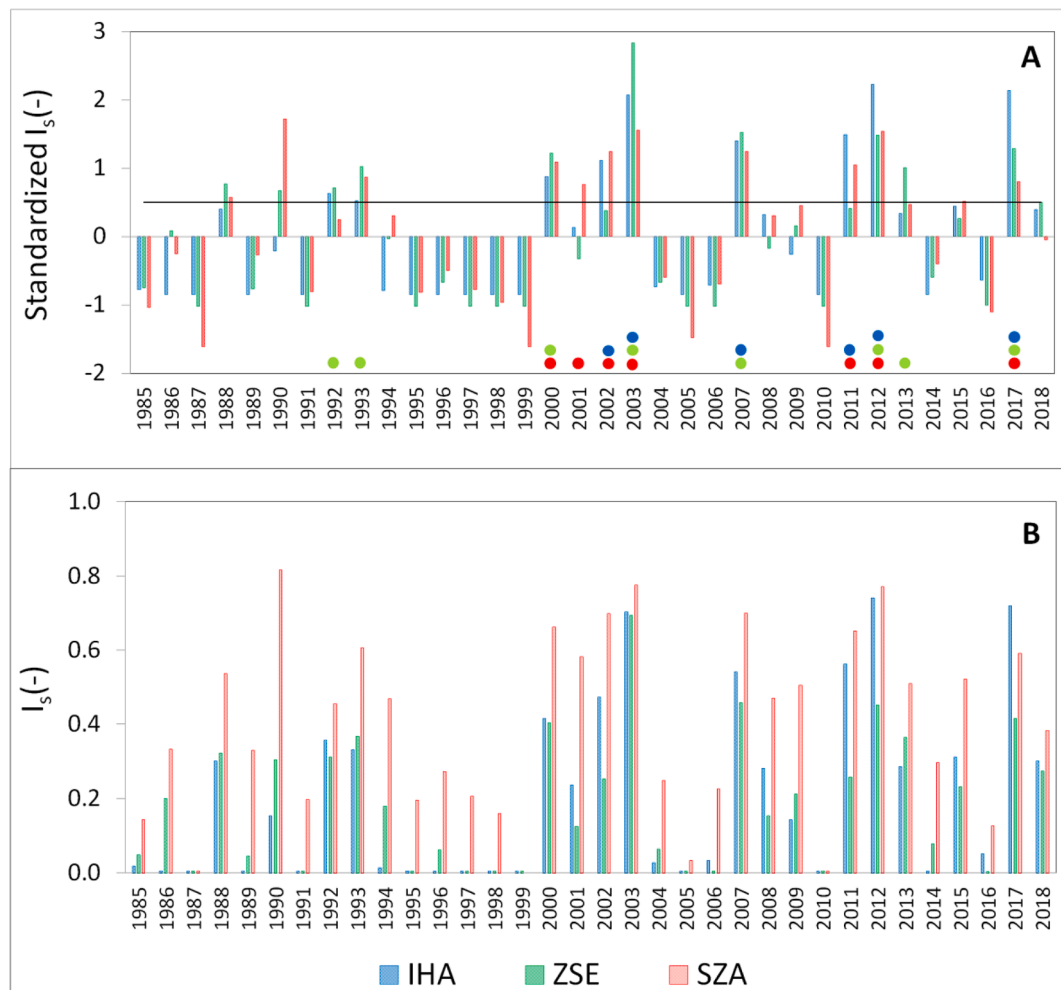


Fig. 6. Standardized (A) and absolute (B) values of the summer water stress index (I_s) for the period 1985–2018, the horizontal solid line denotes the defined threshold of drought (stand. $I_s \geq 0.5$), the coloured points symbolise the selected drought periods for the sites.

result in decreased carbohydrates reserves and thus lower growth rates after drought (Michelot et al., 2012). Additionally, Tognetti et al. (2007) reported that QC was drought tolerant based on measurements of water-use efficiency and water status that were also consistent with tree-ring records of this species in Italy. Similarly, changes of sap flow and stem radius increment in a mature mixed oak stand showed that QC exhibited much higher (+38%) mean daytime sap flow density and lower (−42%) stem water deficit during the same drought period than QP in Hungary (Mészáros et al., 2011). Formerly reported ecophysiological data and our measured tree-ring records refer to a more drought-tolerant characteristic of QC compared to QP, probably because of its more conservative use of soil water. Although phenotypic plasticity of the species and other environmental factors may be relevant, the interaction of water-use strategy of QP and QC and water availability of topsoils is a strong determinant of the growth performance of these species in south-western Hungary.

In addition, species with low drought resistance for radial growth such as QC in our study may change biomass allocation into roots to improve access to water and nutrients. After the drought event, the allocation may rearrange again to rebalance the root and shoot biomass (McCarthy and Enquist, 2007). Accounting for this process, the radial growth of trees may not reflect the whole tree performance under drought stress (Pretzsch et al., 2012b). Additionally, Hoffmann et al. (2018) found that quantifying drought sensitivity based solely on breast height measures may result in biased estimates of production declines since the growth response of species reduced from lower to upper stem

height. Although the growth reaction patterns (resistance, recovery) for younger trees might be less distinct than for older trees (Candel-Pérez et al., 2012), in our study we received different growth reaction of the analysed species thus stress response patterns may be more species-specific than age-dependent (Linares and Tiscar, 2010).

Although our results suggest different radial growth reactions of the analysed species to droughts it is hard to categorize them clearly as an isohydric or an anisohydric species based solely on radial growth measurements. At most, growth responses indicate different growth plasticity of these species.

The sum of the total growth loss (TGR) of all stands and drought periods was higher for QC (5.36) than for QP (5.08), but the difference was not significant ($t = 0.47$, $p < 0.05$). The sum of the recovery years considering all stands and drought periods was similar for both species with 21 and 22 years for QC and QP, respectively.

We found that the ratio of TGR and I_s was rather stable for QC with a slightly decreasing tendency towards more arid climatic conditions with values between 0.39 and 0.44 meaning that the response of QC was in a linear relationship with the severity of the droughts. In the case of QP, we found ratio values for the more humid sites IHA and ZSE with values 0.41 and 0.56 while it decreased to 0.26 in the case of the more arid site SZA. The possible interpretation of these results could be that the two species reacted similarly to soil water stress in moister sites but the decline of the ratio of TGR and I_s in the case of QP indicated lower sensitivity and thus lower growth plasticity to droughts.

The relation of resistance and recovery of the species was computed

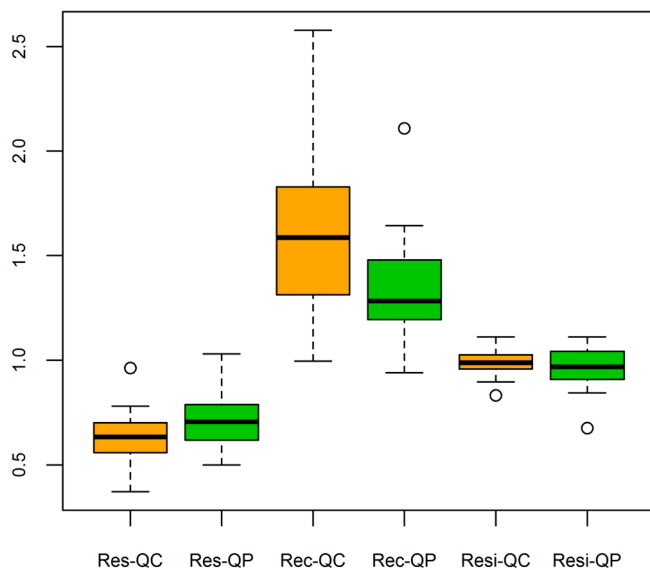


Fig. 7. Drought indices after Lloret et al. (2011) of the two oak species for all drought events ($n = 13$; Res: resistance, Rec: recovery, Resi: resilience); thick lines are the medians, the upper and lower limits of the boxes represent the first and the third quartiles respectively, the whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the top (bottom) of the box, circles denote the outliers.

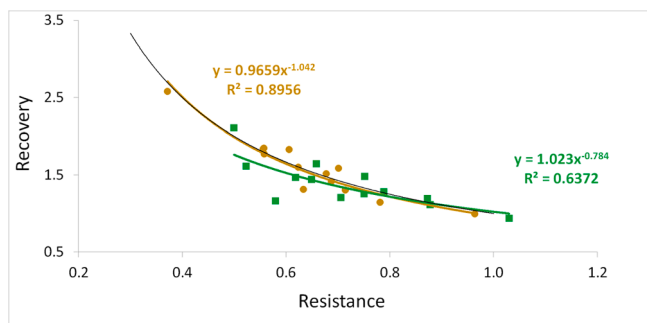


Fig. 8. Comparison of the relationship between resistance and recovery values for QP (green rectangles and line) and QC (orange circles and line) to a hypothetical line of full resilience (black line) (Schwarz et al., 2020). The pairs of resistance and recovery were calculated using 1-year pre-and post-drought growth conditions for all available drought periods ($n = 13$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using one-year pre-and post-drought growth for all drought periods. We used the exponential function that provided the best fit to the data (QC: spearman- $r = 0.94$, residual SE = 0.16; QP: spearman- $r = 0.66$, residual SE = 0.2). The recovery values of the theoretical 'line of full resilience' were expressed as the ratio of unity and resistance values ranging from 0.3 to 1 (Fig. 8). The relationship revealed that for lower resistance values the recovery of QC was mainly higher than for QP and closely followed the theoretical 'line of full resilience' (Schwarz et al., 2020) suggesting the higher drought resilience of QC (ANOVA $p < 0.01$). Unfortunately, in our analysis no particularly low resistance values of QP could have been included thus we could not explore how this species would have recovered.

4. Conclusions

Two oak species (*Quercus petraea* (Matt.) Liebl. and *Quercus cerris* L.) were investigated with respect to their drought sensitivity in young

forest stands along a precipitation gradient in Hungary using dendrochronological metrics. Despite the relatively short dendrochronological series (20–31 years), we could evaluate the effect of several drought periods on radial growth of sessile oak and Turkey oak.

Our study revealed that summer water availability was the main limiting factor on radial growth of both species regardless of the climatic condition of the sites. The growth response of sessile oak and Turkey oak trees to drought conditions suggested markedly different strategies. Turkey oak responded dynamically to the available soil water content with substantially reduced growth rates during droughts, thus probably saving reserves for post-drought recovery and survival. On the other hand, sessile oak showed sustained levels of growth during drought events by likely utilizing probably its reserves and thus could recover slower after drought events. Growth response of sessile oak reduced, moreover, substantially along the climatic gradient of the study sites indicating lower growth plasticity of sessile oak to droughts towards more arid conditions.

As a consequence, sessile oak may be more prone to sooner decline due to successive droughts than Turkey oak since it may not be able to recover fully between successive drought events. We propose that future studies should aim to evaluate whether drought sensitivity traits of different dominant forest tree species are getting more deteriorate if trees of various age classes experience successive droughts and to compare these traits among the different species.

CRedit authorship contribution statement

Norbert Mórícz: Conceptualization, Writing - original draft, Writing - review & editing. **Gábor Illés:** Conceptualization, Writing - review & editing. **Ilona Mészáros:** Writing - review & editing. **Balázs Garamszegi:** Writing - review & editing. **Imre Berki:** Conceptualization. **Zsófia Bakacsi:** . **József Kámpel:** . **Orsolya Szabó:** Writing - review & editing. **Ervin Rasztovtovits:** Writing - review & editing. **Klára Cseke:** Writing - review & editing. **Katalin Bereczki:** . **Tamás Márton Németh:** Conceptualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the local forest management (SEFAG Forest Management and Wood Industry Share Co., branch office Iharos, Zselic and Szántód) for their valuable support in field-work. We also thank for the MTA Institute for Soil Sciences and Agricultural Chemistry and the soil laboratory of the NAIK Forest Research Institute for soil analysis. Additionally, we thank Anikó Hirka, who provided the biotic damage data. Finally, we express our gratitude to the anonymous Reviewer for constructive criticism. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

- Árvai, M., Morgós, A., Kern, Z., 2018. Growth-climate relations and the enhancement of drought signals in Pedunculate oak (*Quercus robur* L.) tree-ring chronology in Eastern Hungary. *IForest* 11 (2), 267–274. <https://doi.org/10.3832/for2348-011>.
- Bertini, G., Amoriello, T., Fabbio, G., Piovosi, M., 2011. Forest growth and climate change: Evidences from the ICP-Forests intensive monitoring in Italy. *IForest* 4 (6), 262–267. <https://doi.org/10.3832/for0596-004>.
- Beguieria, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *Int. J. Climatol.* 34 (10), 3001–3023. <https://doi.org/10.1002/joc.3887>.

- Brèteau-Amores, S., 2018. Drought effects on early growth and mortality of three oak species in the Upper Rhine Valley. *Am. J. Clim. Change* 7 (1), 336–354. <https://doi.org/10.4236/ajcc.2018.72020>.
- Briffa, K.R., Jones, P.D., Wigley, T.M.L., Pilcher, J.R., Baillie, M.G.L., 1983. Climate reconstruction from tree rings: Part 1, basic methodology and preliminary results for England. *Int. J. Climatol.* 3 (3), 233–242. <https://doi.org/10.1002/joc.3370030303>.
- Brodrick, T.J., Powers, J., Cochard, H., Choat, B., 2020. Hanging by a thread? Forests and drought. *Science* 368 (6488), 261–266. <https://doi.org/10.1126/science.aat7631>.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26 (2), 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Busotti, F., Pollastrini, M., 2017. Traditional and novel indicators of climate change impacts on European forest trees. *Forests* 8 (4), 137. <https://doi.org/10.3390/f8040137>.
- Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R., Sánchez-Miranda, A., Granda, E., Serra-Malquer, X., Ibáñez, R., 2018. Forest growth responses to drought at short- and long-term scales in Spain: Squeezing the stress memory from tree rings. *Front. Ecol. Evol.* 6, 1–11. <https://doi.org/10.3389/fevo.2018.00009>.
- Candel-Pérez, D., Linares, J.C., Vinegla, B., Lucas-Borja, M.E., 2012. Assessing climate-growth relationships under contrasting stands of co-occurring Iberian pines along an altitudinal gradient. *For. Ecol. Manage.* 274, 48–57.
- Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A. W., Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M., Schwartz, M.W., Waring, K.M., Zimmermann, N.E., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Glob. Chang. Biol.* 22 (7), 2329–2352. <https://doi.org/10.1111/gcb.13160>.
- Cavin, L., Jump, A.S., 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Glob. Chang. Biol.* 23 (1), 362–379. <https://doi.org/10.1111/gcb.13366>.
- Cook, R.D., Weisberg, S., 1982. *Residuals and influence in regression*. Chapman and Hall, New York.
- Cufar, K., Grabner, M., Morgós, A., del Castillo, E.M., Merela, M., de Luis, M., 2014. Common climatic signals affecting oak tree-ring growth in SE Central Europe. *Trees* 28 (5), 1267–1277. <https://doi.org/10.1007/s00468-013-0972-z>.
- Cutini, A., 1997. Drought effects on canopy properties and productivity in thinned and unthinned Turkey Oak stands. *Plant Biosyst.* 131 (1), 59–65. <https://doi.org/10.1080/11263504.1997.10654167>.
- Csóka, Gy., Hírka, A., 2009. Recent outbreaks of Gypsy moth (*Lymantria dispar* L.) in Hungary. *Növényvédelem* 45(4), 196–201. (in Hungarian).
- Diedenhofen, B., Musch, J., 2015. cocor: A comprehensive solution for the statistical comparison of correlations. *PLoS ONE* 10 (4), e0121945. <https://doi.org/10.1371/journal.pone.0121945>.
- Friedrichs, D.A., Büntgen, U., Frank, D.C., Esper, J., Neuwirth, B., Löffler, J., 2009. Complex climate controls on 20th century oak growth in Central-West Germany. *Tree Physiol.* 29 (1), 39–51. <https://doi.org/10.1093/treephys/tpn003>.
- Führer, E., Horváth, L., Jagodics, A., Machon, A., Szabados, I., 2011. Application of a new aridity index in Hungarian forestry practice. *Időjárás* 115, 103–118.
- Gazol, A., Camarero, J.J., Anderegg, W.R.L., Vicente-Serrano, S.M., 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Glob. Ecol. Biogeogr.* 26 (2), 166–176. <https://doi.org/10.1111/geb.12526>.
- Gieger, T., Thomas, F.M., 2005. Differential response of two Central-European oak species to single and combined stress factors. *Trees* 19 (5), 607–618. <https://doi.org/10.1007/s00468-005-0424-5>.
- Giuggiola, A., Kuster, T.M., Saha, S., 2010. Drought-induced mortality of Scots pines at the southern limits of its distribution in Europe: causes and consequences. *IForest* 3 (4), 95–97. <https://doi.org/10.3832/for0542-003>.
- Granier, A., Bréda, N., Biron, P., Villet, S., 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecol. Modell.* 116 (2–3), 269–283. [https://doi.org/10.1016/S0304-3800\(98\)00205-1](https://doi.org/10.1016/S0304-3800(98)00205-1).
- Gulyás, K., Mórincz, N., Rasztovits, E., Horváth, A., Balázs, P., Berkli, I., 2019. Accelerated height growth versus mortality of *Quercus petraea* (Matt.) Liebl. in Hungary. *South-east Eur. for.* 10 (1), 1–7. <https://doi.org/10.15177/seeor.19-01>.
- Gustafson, E.J., Sturtevant, B.R., 2013. Modeling forest mortality caused by drought stress: Implications for climate change. *Ecosystems* 16 (1), 60–74. <https://doi.org/10.1007/s10021-012-9596-1>.
- Günthardt-Goerg, M.S., Kuster, T.M., Arend, M., Vollenweider, P., 2013. Foliage response of young central European oaks to air warming, drought and soil type. *Plant Biol.* 15 (S1), 185–197. <https://doi.org/10.1111/j.1438-8677.2012.00665.x>.
- Haylock, M., Hofstra, N., Tank, A.K., 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *J. Geophys. Res.* 113, D20119. <https://doi.org/10.1029/2008.JD010201>.
- Härdt, W., Niemeyer, T., Assmann, T., Aullinger, A., Fichtner, A., Lang, A., Leuschner, C., Neuwirth, B., Pfister, L., Quante, M., Ries, C., Schuldt, A., von Oheimb, G., 2013. Climatic responses of tree-ring width and $\delta^{13}C$ signatures of sessile oak (*Quercus petraea* Liebl.) on soils with contrasting water supply. *Plant Ecol.* 214 (9), 1147–1156. <https://doi.org/10.1007/s11258-013-0239-1>.
- Hírka, A., 2006. Biotic and abiotic damage in the Hungarian forests in 2005, and the damage forecast for 2006. Hungarian Forest Research Institute, Budapest (in Hungarian).
- Hoffmann, N., Schall, P., Ammer, C., Leder, B., Vor, T., 2018. Drought sensitivity and stem growth variation of nine alien and native tree species on a productive forest site in Germany. *Agric. For. Meteorol.* 256–257, 431–444. <https://doi.org/10.1016/j.agrformet.2018.03.008>.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- IPCC, 2018. Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [V. Masson-Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J. Skea, P.R.Shukla, A. Pirani, W. Moufouma-Okia, C.Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, T. Waterfield(eds.)]. In Press.
- Jakucs, P., Mészáros, I., Papp, B.L., Tóth, J.A., 1986. Acidification of soil and decay of sessile oak in the “Sikfőkút Project” area (N-Hungary). *Acta Bot. Hung.* 32 (1–4), 303–322.
- Kern, Z., Patkó, M., Kázmér, M., Fekete, J., Kele, S., Pályi, Z., 2013. Multiple tree-ring proxies (earlywood width, latewood width and $\delta^{13}C$) from pedunculate oak (*Quercus robur* L.). Hungary. *Quat. Int.* 239, 257–267. <https://doi.org/10.1016/j.quaint.2012.05.037>.
- Klapwijk, M.J., Csóka, G., Hírka, A., Björkman, C., 2013. Forest insects and climate change: long-term trends in herbivore damage. *Ecol. Evol.* 3 (12), 4183–4196. <https://doi.org/10.1002/ece3.717>.
- Kolár, T., Cermák, P., Trnka, M., Zid, T., Rybníček, M., 2017. Temporal changes in the climate sensitivity of Norway spruce and European beech along an elevation gradient in Central Europe. *Agric. For. Meteorol.* 239, 24–33. <https://doi.org/10.1016/j.agrformet.2017.02.028>.
- Kovács, I.P., Czifány, S.z., 2017. The effect of climate and soil moisture on the tree-ring pattern of Turkey oak (*Quercus cerris* L.) in Central Transdanubia, Hungary. *Időjárás* 121 (3), 243–263.
- Kunz, J., Löffler, G., Bauhus, J., 2018. Minor European broadleaved tree species are more drought-tolerant than *Fagus sylvatica* but not more tolerant than *Quercus petraea*. *For. Ecol. Manage.* 414, 15–27. <https://doi.org/10.1016/j.foreco.2018.02.016>.
- Levanič, T., Cáter, M., McDowell, N.G., 2011. Associations between growth, wood anatomy, carbon isotope discrimination and mortality in a *Quercus robur* forest. *Tree Physiol.* 31 (3), 298–308. <https://doi.org/10.1093/treephys/tpq111>.
- Linares, J.C., Tiscar, P.A., 2010. Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. *Tree Physiol.* 30, 795–806. <https://doi.org/10.1093/treephys/tpq052>.
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120 (12), 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>.
- Martínez-Vilalta, J., Poyatos, R., Aguadé, D., Retana, J., Mencuccini, M., 2014. A new look at water transport regulation in plants. *New Phytol.* 204 (1), 105–115. <https://doi.org/10.1111/nph.12912>.
- Mátyás, C.s., Berkli, I., Bidló, A., Csóka, G.y., Czímber, K., Führer, E., Gálos, B., Gribovszki, Z., Illés, G., Hírka, A., Somogyi, Z., 2018. Sustainability of forest cover under climate change on the temperate-continental xeric limits. *Forests* 9, 489. <https://doi.org/10.3390/f9080489>.
- McCarthy, M.C., Enquist, B.J., 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Funct. Ecol.* 21 (4), 713–720. <https://doi.org/10.1111/j.1365-2435.2007.01276.x>.
- Mérián, P., Pierrat, J., Lebourgeois, F., 2013. Effect of sampling effort on the regional chronology statistics and climate-growth relationships estimation. *Dendrochronologia* 31 (1), 58–67. <https://doi.org/10.1016/j.dendro.2012.07.001>.
- Mészáros, I., Kanalas, P., Fenyvesi, A., Kis, J., Nyitrai, B., Szöllösi, E., Oláh, V., Demeter, Z., Lakatos, Á., Ander, I., 2011. Diurnal and seasonal changes in stem radius increment and sap flow density indicate different responses of two co-existing oak species to drought stress. *Acta Silv. et Lignaria Hungarica* 7, 97–108.
- Mészáros, I., Veres, S., Szöllösi, E., Koncz, P., Kanalas, P., Oláh, V., 2008. Responses of some ecophysiological traits of Sessile oak (*Quercus petraea*) to drought stress and heat wave in growing season of 2003. *Acta Biol. Szeged.* 52 (1), 107–109.
- Michelot, A., Simard, S., Rathgeber, C., Dufrene, E., Damesin, C., 2012. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol.* 32 (8), 1033–1045. <https://doi.org/10.1093/treephys/tps052>.
- Mirfenderesgi, G., Matheny, A.M., Bohrer, G., 2019. Hydrodynamic trait coordination and cost-benefit trade-offs throughout the isohydric-anisohydric continuum in trees. *Ecohydrology* 12 (1), e2041. <https://doi.org/10.1002/eco.2041>.
- Mishra, A.K., Singh, V.P.A., 2010. Review of drought concepts. *J. Hydrol.* 391 (1–2), 202–216. <https://doi.org/10.1016/j.jhydrol.2010.07.012>.
- Misi, D., Náfrádi, K., 2017. Growth response of Scots pine to changing climatic conditions of the last 100 years: a case study from Western Hungary. *Trees* 31, 919–928. <https://doi.org/10.1007/s00468-016-1517-z>.
- Moreno, A., Hasenauer, H., 2015. Spatial downscaling of European climate data. *Int. J. Climatol.* 36 (3), 1444–1458. <https://doi.org/10.1002/joc.4436>.
- Mórincz, N., Garamszegi, B., Rasztovits, E., Bidló, A., Horváth, A., Jagiczka, A., Illés, G., Vekerdy, Z., Somogyi, Z., Gálos, B., 2018. Recent drought-induced vitality decline of Black Pine (*Pinus nigra* Arn.) in South-West Hungary – Is this drought-resistant species under threat by climate change? *Forests* 9, 414. <https://doi.org/10.3390/f9070414>.
- Nardini, A., Lo Gullo, M.A., Saelleo, S., 1999. Competitive strategies for water availability in two Mediterranean *Quercus* species. *Plant Cell. Environ.* 22 (1), 109–116. <https://doi.org/10.1046/j.1365-3040.1999.00382.x>.
- Nechita, C., Popa, I., Eggertsson, Ó., 2017. Climate response of oak (*Quercus* spp.), an evidence of a bioclimatic boundary induced by the Carpathians. *Sci. Total Environ.* 599–600, 1598–1607. <https://doi.org/10.1016/j.scitotenv.2017.05.118>.

- Peltier, D.M.P., Fell, M., Ogle, K., 2016. Legacy effects of drought in the southwestern United States: A multi-species synthesis. *Ecol. Monogr.* 86 (3), 312–326. <https://doi.org/10.1002/ecm.1219>.
- Péczely, G.y., 1979. Éghajlattan. Tankönyvkiadó, Budapest.
- Pretzsch, H., Schütze, G., Uhl, E., 2012a. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* 15 (3), 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>.
- Pretzsch, H., Uhl, E., Biber, P., Schütze, G., Coates, D., 2012b. Change of allometry between coarse root and shoot of Lodgepole pine (*Pinus contorta* DOUGL. ex. LOUD.) along a stress gradient in the sub-boreal forest zone of British Columbia. *Scand. J. For. Res.* 27 (6), 532–544. <https://doi.org/10.1080/02827581.2012.672583>.
- R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/>.
- Rasztovits, E., Berki, I., Mátyás, C.s., Czimmer, K., Pötzelsberger, E., Móríc, N., 2014. The incorporation of extreme drought events improves models for beech persistence at its distribution limit. *Ann. For. Sci.* 71, 201–210. <https://doi.org/10.1007/s13595-013-0346-0>.
- Instruments, R., 2014. WinDENDRO for Tree-ring Analysis. Canada Inc, Québec.
- Rybníček, M., Čermák, P., Prokop, O., Žid, T., Trnka, M., Kolář, T., 2016. Oak (*Quercus* spp.) response to climate differs more among sites than among species in central Czech Republic. *Dendrobiology* 75, 55–65. <https://doi.org/10.12657/denbio.075.006>.
- Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C. & Wilmking, M., 2011. Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *For. Ecol. Manage.* 262 (6), 947–961. <https://doi.org/10.1016/j.foreco.2011.05.026>.
- Schuld, B., Buras, A., Arend, M., Vitas, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T.E.E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübke, T., Nelson, D.B., Rammig, A., Rigling, A., Rose, L., Ruehr, N.K., Schumann, K., Weiser, F., Werner, C., Wohlgemuth, T., Zang, C.S., Kahmen, A., 2020. A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic Appl. Ecol.* 45, 86–103. <https://doi.org/10.1016/j.baae.2020.04.003>.
- Schwarz, J., Skiadas, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought—a critique of commonly used resilience indices and recommendations for future studies. *Curr. For. Rep.* 6 (3), 185–200. <https://doi.org/10.1007/s40725-020-00119-2>.
- Somogyi, Z., Koltay, A., Molnár, T., Móríc, N., 2018. Forest health monitoring system in Hungary based on MODIS products. IX. Theory meets practice in GIS.
- Speer, J., 2010. The Fundamentals of Tree-Ring Research. The University of Arizona Press, Tucson, Arizona.
- Spinoni, J., Naumann, G., Vogt, J., Barbosa, P., 2015. European drought climatologies and trends based on a multi-indicator approach. *Glob. Planet Change.* 127, 50–57. <https://doi.org/10.1016/j.gloplacha.2015.01.012>.
- Stand-based inventory; National Forestry Database; Unpublished data, 2010.
- Stojanović, D.B., Levanić, T., Matović, B., Stjepanović, S., Orlović, S., 2018. Growth response of different tree species (oaks, beech and pine) from SE Europe to precipitation over time. *Dendrobiology* 79, 97–110. <https://doi.org/10.12657/denbio.079.009>.
- Szalai, S., Auer, I., Hiebl, J., Milkovich, J., Radim, T., Stepanek, P., Zahradnicek, P., Bihari, Z., Lakatos, M., Szentimrey, T., Limanowka, D., Kilar, P., Cheval, S., Deak, Gy., Mihic, D., Antolovic, I., Mihajlovic, V., Nejedlik, P., Stastny, P., Mikulova, K., Nabyvanets, I., Skryryk, O., Krakovskaya, S., Vogt, J., Antofie, T. & Spinoni, J., 2013. Climate of the Greater Carpathian region. Final Technical Report. www.carpatclim.eu.org.
- Thornthwaite, C., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38 (1), 55–94. <https://doi.org/10.2307/210739>.
- Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. *For. Ecol. Manage.* 376, 205–220. <https://doi.org/10.1016/j.foreco.2016.06.020>.
- Tognetti, R., Raschi, A., Béres, C., Fenyvesi, A., Ridder, H.W., 1996. Comparison of sap flow, cavitation and water status of *Quercus petraea* and *Quercus cerris* trees with special reference to computer tomography. *Plant Cell. Environ.* 19 (8), 928–938. <https://doi.org/10.1111/j.1365-3040.1996.tb00457.x>.
- Tognetti, R., Cherubini, P., Marchi, S., Raschi, A., 2007. Leaf traits and tree rings suggest different water-use and carbon assimilation strategies by two co-occurring *Quercus* species in a Mediterranean mixed-forest stand in Tuscany, Italy. *Tree Physiol.* 27, 1741–1751.
- Van der Werf, G.W., Sass-Klaassen, U.G.W., Mohren, G.M.J., 2007. The impact of the 2003 summer drought on the intra-annual growth pattern of beech (*Fagus sylvatica* L.) and oak (*Quercus robur* L.) on a dry site in the Netherlands. *Dendrochronologia* 25, 103–112.
- Vanhellemont, M., Sousa-Silva, R., Maes, S.L., Van den Bulcke, J., Hertzog, L., De Groote, S.R.E., Van Acker, J., Bonte, D., Martel, A., Lens, L., Verheyen, K., 2019. Distinct growth responses to drought for oak and beech in temperate mixed forests. *Sci. Total Environ.* 650 (2), 3017–3026. <https://doi.org/10.1016/j.scitotenv.2018.10.054>.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscale drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *J. Clim.* 23 (7), 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>.
- Weber, P., Bugmann, H., Pluess, A.R., Walthert, L., Rigling, A., 2013. Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees: Structure and Function* 27 (1), 171–181. <https://doi.org/10.1007/s00468-012-0786-4>.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Appl. Meteorol. Climatol.* 23 (2), 201–213. [https://doi.org/10.1175/1520-0450\(1984\)023<0201:OTAVOC>2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2).
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E. R., Gangadagamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Chang.* 3, 292–297. <https://doi.org/10.1038/nclimate1693>.
- Zimmermann, J., Hauck, M., Dulamsuren, C., Leuschner, C., 2015. Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in Central European mixed forests. *Ecosystems* 18, 560–572. <https://doi.org/10.1007/s10021-015-9849-x>.