Oak decline induced by mistletoe, competition and climate change: a case study from central Europe

Vliv ochmetu, kompetice a klimatických změn na růst a odumíraní dubů: případová studie ze střední Evropy

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It is predicted that rising temperatures and extreme summer droughts will adversely affect the growth of pedunculate oak (*Quercus robur*) and contribute to local population decline. Furthermore, such oaks may become prone to infestation with mistletoe (*Loranthus europaeus*) and competition from neighbouring trees. We tested these predictions in the warm, south-eastern part of the Czech Republic, a drought-prone area where oaks die prematurely. We compared the radial growth patterns of eight categories of oaks differing in age (younger or older than 60 years), presence of neighbouring trees (solitary versus grouped) and infestation with mistletoe (infested versus healthy), and their responses to variation in both annual and intra-annual temperature (T) and precipitation (P). We analysed long-term data from tree rings and detailed dendrometer records of daily increments using moving correlations and regression trees. Oak growth is affected by (i) dry and cold winters, resulting in root damage and water shortages during summer, (ii) a cool and wet March–April, hampering the onset of earlywood growth, and (iii) a hot and dry May–July period, reducing latewood formation. Latewood width increases when February P > 55 mm, March T > 3.3 °C, April P < 60 mm, May P > 50 mm, June T < 19 °C and August P > 40 mm. Latewood width decreases with tree age, mistletoe infestation and competiton from neighbouring trees. These factors are responsible for different climate–growth responses. Infested oaks develop less latewood if T in June–July is high and this is associated with drought. In healthy oaks May P determines how quickly earlywood growth is completed and hence when latewood formation starts. Grouped trees that compete for soil water are more prone to June–July droughts but less harmed by cold springs than solitary oaks. Dendrometer records show that the net daily increments (ΔR) recorded for oaks growing in groups are mainly associated with water deficit, whereas those of solitary oaks with high summer T, which fluctuates more in open landscape than in woods, resulting in a reduced number of days with a positive ΔR. However, under optimal conditions (soil moisture > 20%, mean daily T 10–20 °C), the ΔR phase recorded for solitary oaks is longer than for oaks in groups, which results in greater annual increments. Hence, the differences between solitary oaks and those in groups is due to a difference in the period of time they spend growing rather than the speed of growth. Infested oaks have smaller ΔRs and annual increments because they grow for a shorter period rather than differences in metabolic activity. These results provide support for the crucial role of climate change (decline in rainfall and increase in summer temperatures over the last three decades) and biotic interactions (mistletoe hemiparasites, inter-tree competition) in oak growth and population decline.

K e y w o r d s: conditional inference trees, dendrometers, moving response function, growth–climate relationships, intra-annual variation, *Loranthus europaeus*, *Quercus robur*, stem contraction, tree–water relations

Introduction

Pedunculate oak (*Quercus robur* L.), a dominant species in European hardwood forests (Dimopoulos et al. 2005), is declining in many regions of its native range (Popa et al. 2013, Rozas & Sampedro 2013, Sohar et al. 2014a, Helama et al. 2016). According to Manion (1981), oak decline is a complex issue that can be attributed to long-term predisposing factors (e.g. tree age, competition, climatic trends, soil conditions, topography), short-term inciting factors (e.g. acute drought, defoliating insects) and contributing factors that further reduce its vigour (e.g. pathogens, infection with mistletoe) (see also Jung et al. 1996, Gibbs & Greig 1997, Rozas & Sampedro 2013). Extreme climatic events including heat stress and summer droughts are considered to be the main factors promoting oak decline in many places in Europe (Dwyer et al. 1995, Siwecki & Ufnalski 1998, Doležal et al. 2010, Sohar et al. 2014a).

Europe has experienced higher average temperatures and increasing incidence of droughts over the last three decades (OECD 2013), but it is unclear whether this has contributed to the decline of oak. The growth of pedunculate oak is generally limited by water availability throughout its entire European distribution. This is documented for Spain (Rozas 2005, 2015), France (Lebourgeois et al. 2004), Slovenia (Čufar et al. 2008), Romania (Popa et al. 2013), the British Isles (Pilcher & Gray 1982), Sweden (Drobyshev et al. 2008), Poland (Bednarz & Ptak 1990), Estonia (Sohar et al. 2014b), Finland (Helama et al. 2009) and the Czech Republic (Doležal et al. 2010, Rybníček et al. 2015). While the vulnerability of oak to water stress is common throughout Europe, high summer temperature has a mixed effect as it impairs tree growth in southern and central Europe, but may favour it at the northern edge of its distribution.

Previous studies reveal the need for more detailed comparative studies of the effect of internal and external factors on the growth of oak of different ages growing in different habitats. This paper aims to explore the effect on the growth of pedunculate oak of age, competition and mistletoe infestation, and these tree's responses to both annual and intra-annual variation in the climate in the warm, south-eastern part of the Czech Republic. This area is renowned for its high plant and insect diversity associated with grasslands, and scattered oak trees and small woodlands, many of the trees in which over the last three decades have died prematurely (Jongepierová 2008). Extreme climatic events such as summer drought, together with increasing rates of mistletoe (*Loranthus europaeus* Jacq.) infection, are hypothesized as factors responsible for the recent decline in oak abundance (Doležal et al. 2010). Mistletoes are highly specialized perennial flowering plants adapted to a parasitic life on the aerial parts of their hosts (Glatzel 1983). They disturb a host's water and nutrient balances and reduce its photosynthesis and respiration (Glatzel & Geils 2009, Urban et al. 2012), thus debilitating infected trees. Severe mistletoe infection may seriously damage or even kill trees (Matula et al. 2015).

The climatic factors that affect tree growth are usually studied by determining the relationships between tree-ring residual chronology and climate using simple correlations or response functions (Zang & Biondi 2015). These methods assume linear relationships between growth and climate. However, as with many other biological processes, the relationship between growth and climate is non-linear, i.e. the best performance is achieved when the temperature or water regimes are optimal. This can be studied using non-linear regressions such as conditional inference trees (Hothorn et al. 2006). These may prove

particularly useful when tree growth–climate relations do not remain constant over time. This is likely to be the case for European trees given the unprecedented change in climate that has occurred over the last century. The longest meteorological records for central Europe show positive trends in mean spring, autumn and winter temperatures over the last century, with accelerated warming since the 1990s (Doležal et al. 2010); the 1990s were the warmest interval in the last 150 years. These records also reveal that there was less rainfall in the second half of 20th century, with a particular decrease in spring and summer rainfall in last three decades.

We studied the growth–climate responses of eight groups of trees categorized in terms of their age (young, old), habitat (solitary trees not subject to competition from neighbouring trees and those growing in groups), and rate of mistletoe infestation (low, high). We hypothesized that (i) trees subject to competition from neighbouring trees will grow less and be more prone to extreme climatic events than solitary trees; (ii) healthy young trees will tolerate a few mistletoe plants with little harmful effect, while old trees that are heavily infested with mistletoe may become less vigorous and are possibly killed or retarded in their growth if subjected to additional stress from drought or extreme temperatures. First, we compared ring widths in average chronologies for eight groups of trees in two contrasting periods; 1988–2009, which was drier and warmer than 1966–1988. Second, in order to determine growth–climate responses we used both traditional dedroclimatological methods (response function, moving correlations) and a new way of analysing non-linear responses. Third, as an alternative to the long-term variation in tree-rings, we continuously monitored intra-annual growth during the vegetative period using detailed information on a tree's reaction to short term changes in climatic conditions during the years 2012 and 2013, collected using automatic belt dendrometers.

Study area

The research was carried out in the main part of the National Nature Reserve at Čertoryje in the White Carpathians Protected Landscape Area (PLA, 748 km^2), a hilly (maximum altitude 970 m a.s.l.) chain formed by base-rich flysch sediments, adjoining the Czech/Slovak border. The region includes villages in narrow valleys, steep slopes covered by deciduous woodlands and grasslands on shallow slopes and plateaus. Due to the remoteness of the area, the region was the last in the Czech Republic to be affected by the communist-era land consolidation and small private farmers retained their land until the early 1980s. Their traditional use of the land created and maintained mosaics of meadows, pastures, small fields, orchards and patches of woodland. Grasslands cover 20% of the PLA, mainly as wooded 'Carpathian meadows', which are famed for their exceptional plant richness and great diversity of *Lepidoptera* (Jongepierová 2008, Merunková et al. 2012, Chytrý et al. 2015). Mean annual temperatures were 8.8 °C, 8.5 °C and 9.1 °C, and mean annual precipitation was 699 mm, 727 mm and 674 mm, respectively, during the periods 1900–2006, 1900–1950 and 1951–2006.

Methods

Data collection and definition of groups

The sampling was carried out in 2006 and 2009 at an altitude of 430–440 m a.s.l., on a west-facing slope in the Čertoryje NNR with an inclination of about 5° (Electronic Appendix 1). Soils here are relatively deep and calcium-rich, drying out in summer. The core samples were collected from single-stemmed oak trees at breast height using 20–50 cm long increment borers. Forty-five solitary trees and 65 trees growing in groups were sampled. Solitary trees were unshaded and usually without neighbours up to a distance of at least 20 m, while the trees growing in groups had close neighbours and their crowns partly overlapped. Core samples from solitary trees and those growing in groups were further categorized in terms of the age of the tree and its degree of mistletoe infestation. Trees under 60 years old were classed as 'young' and those over 60 years as 'old'. The number of mistletoe plants on each of the trees from which a core was collected were counted; trees with fewer than 5 small plants were classified as lightly infested (LMI) and those with more than 5 (up to a maximum of 15 plants on a single tree) were classified as heavily infested (HMI) (Table 1). By combining these criteria, eight groups were created.

Table 1. – Characteristics of tree-ring data. Average values are presented and values in parentheses denote standard deviations. LW – latewood, AC – first-order autocorrelation, MS – mean sensitivity, EPS – expressed population signal. LMI – low mistletoe infestation, HMI – high mistletoe infestation.

			No. trees	Age [year]	AC	MS	EPS	Period
Solitary	young	LMI	6	58 (8)	0.70 (0.12)	0.29	0.90	1962–2009
		HMI	8	61 (4)	0.58 (0.13)	0.29	0.90	1949–2009
	old	LMI	8	80 (13)	0.61 (0.11)	0.30	0.87	1927–2009
		HMI	7	101 (12)	0.60 (0.08)	0.27	0.91	1934–2009
Grouped	young	LMI	17	43 (8)	0.56 (0.16)	0.24	0.89	1952–2009
		HMI	8	60 (6)	0.61 (0.15)	0.24	0.92	1949–2009
	old	LMI	9	86 (19)	0.68 (0.12)	0.21	0.86	1933–2009
		HMI	10	76 (9)	0.65 (0.12)	0.27	0.93	1904–2009

Tree-ring data

The cores were polished with sand paper and early- and latewood tree rings were measured to the nearest 0.01 mm using a TimeTable measuring device and PAST4 software (www.sciem.com). Ring-sequences were cross-dated visually using the pattern of wide and narrow rings, and verified using the PAST4 program and percentage of parallel variation (Gleichläufigkeit). Earlywood increments are usually more sensitive to the previous year's autumn temperature, while latewood increments depend on the climate in the current growing season. Hence, the latewood width mainly determines the total annual increment while the earlywood is more constant in time (Doležal et al. 2010, Sohar et al. 2014a). Hence, the effect of climate on the latewood components of radial growth is expressed.

For the dendroclimatic analysis the latewood time-series were detrended using a negative exponential curve and stabilized with 100-years spline using the dplR R package

(Bunn 2010). First order autocorrelation of the chronologies studied was high and varied between 0.56 and 0.70. It was removed by autoregressive modelling and the resulting residual series were averaged to a mean chronology by computing the biweight robust mean (Electronic Appendix 2). Chronology mean sensitivity ranged between 0.21 and 0.30 and tended to be higher for the solitary trees. Expressed population signal values were above the usually applied threshold of 0.85 (Wigley et al. 1984) and thus indicated that the populations studied were representative, even if some chronologies were for less than 10 trees. Based on a dendrogram (Electronic Appendix 3) produced by hierarchical cluster analysis (applying Euclidean distances between the chronologies grouped by Ward's minimum variance method), two main clusters were identified, which corresponded to the solitary and grouped trees, with the exception of the grouped old HMI oaks.

Climate data

Climate data were obtained from three meteorological stations: Velká nad Veličkou (precipitation records for the period 1961–2009, 250 m a.s.l., 7.5 km from NPR Čertoryje), Strážnice (temperature records for the period 1961–2009, 200 m a.s.l., 10 km from the NPR Čertoryje), and Vienna (temperature records for the period 1775–1995, 140 km from NPR Čertoryje). Furthermore, monthly total precipitation was available for the period 1898–1996 for southern Moravia, which were used for a fir tree-ring reconstruction of March–July precipitation (Brázdil et al. 2002). As climatic data from Velká nad Veličkou and Strážnice were highly correlated with climatic series from Vienna and southern Moravia mean r^2 of 0.87 from linear regressions between Strážnice and Vienna temperatures for the common period 1961–1995, and mean r^2 of 0.64 from linear regressions between Velká nad Veličkou and southern Moravia precipitation for the common period 1961–1996), long-term temperature and precipitation series for these sites were developed from available climatic records using linear regression (Electronic Appendix 4).

Annual variation in the growth–climate relationship

The climatic signal in residual chronologies was first studied for the period 1962–2009 using a simple correlation and bootstrapped response function, which removed multicollinearity between the climatic variables, using the treeclim R package (Zang & Biondi 2015). For this common period monthly data on mean air temperature (T) and sum of precipitation (P) over a 12-month window from September of the previous year to the current August were included in the analysis. To test for temporal stability in the dendroclimatic relationship, 45-year moving correlation coefficients were calculated using four chronologies for old trees for the period 1934–2009. This analysis also captured almost the whole chronologies for old trees. We further used the conditional inference trees to account for the variation in annual growth associated with mean monthly climatic variables. This involves non-parametric regressions and results in a dichotomous tree that indicates the months T and P contribute to growth. This type of classification and regression tree has several crucial advantages over other approaches (e.g. traditional CART algorithm), including (i) the statistical testing of each split by permutation, (ii) no need for problematic pruning of over-fitted trees, and (iii) no selection bias towards variables with many possible splits or missing values (Hothorn et al. 2006).

Intra-annual variation in the growth–climate relationship

To investigate the radial growth of pedunculate oaks in more detail, variation in radius was measured using dendrometers during the vegetative period in 2012 and 2013, together with daily changes in T and P for two solitary old trees with LMI and HMI and one old LMI tree growing in a group of trees. DRL26 automatic band dendrometers (www.emsbrno.cz) with built-in growth and temperature dataloggers were installed 1 m above ground. The instruments measured the displacement of the band with a resolution of less than 1 μm. Data were recorded every hour from 7 February 2012 to 14 February 2014. To supplement this study of the variation in the radius, temperature data were recorded at hourly intervals. As the results for both years were similar, we present mostly those for 2013.

We used the stem cycle approach (Deslauriers et al. 2003) to extract irreversible stem radius increments (Downes et al. 1999, Deslauriers et al. 2007). In fact, dendrometers measure the variation in stem radius, which includes both the irreversible radial increase reflecting growth and the reversible, generally diurnal, rhythms of stem shrinking and swelling due to water loss and uptake (Herzog et al. 1995, Irvine & Grace 1997). A diurnal time series was divided into three circadian phases: contraction (DC the period between the morning stem radius maximum and the afternoon minimum), expansion (DE the total period from the stem radius minimum to the next morning's maximum), and stem radius increment (SRI the part of the expansion phase from the time when the stem radius exceeds the morning maximum until the subsequent maximum). The net daily increment (ΔR) was calculated over the period when the stem radius exceeded the morning maximum until the subsequent maximum. Only positive differences were processed, since they reflect net radial daily increments. Maximum daily shrinkage (MDS) was also calculated as the difference between the morning maximum and afternoon minimum. To assess the causal relationships between water, temperature, phase duration and ΔR and MDS, simple and partial regressions were calculated. In addition, 49-day moving correlation coefficients were calculated between ΔR chronologies and in situ measured air temperature and soil moisture (SM) recorded by TOMST® TMS stations at hourly intervals. The daily climate data were averaged over 2-hour intervals and the moving correlations were similarly calculated as for annual ring increments and monthly climate data. Daily precipitation sums (P) were obtained from the meteorological station Velká nad Veličkou.

Results

Association between absolute growth increments, competition, age and mistletoe infestation

Absolute increments differed between the eight groups of oak trees (Fig. 1), particularly over the last two decades (1988–2009), which were significantly warmer and drier than the previous two decades (1966–1987) (Electronic Appendices 5–6). The conditional inference trees show a significant effect of all three factors (age, habitat, mistletoe) on absolute increment in both periods (Fig. 2 and Electronic Appendix 7), with an increasing importance of mistletoe infestation in the second, drier period. For each age/habitat category, LMI oaks had significantly higher increments than HMI oaks, with the exception of old solitary oaks. The highest increments were recorded for young LMI oaks, followed by young HMI oaks and old LMI oaks; the smallest increments were recorded for grouped old HMI oaks (significant effect of habitat, Fig. 1).

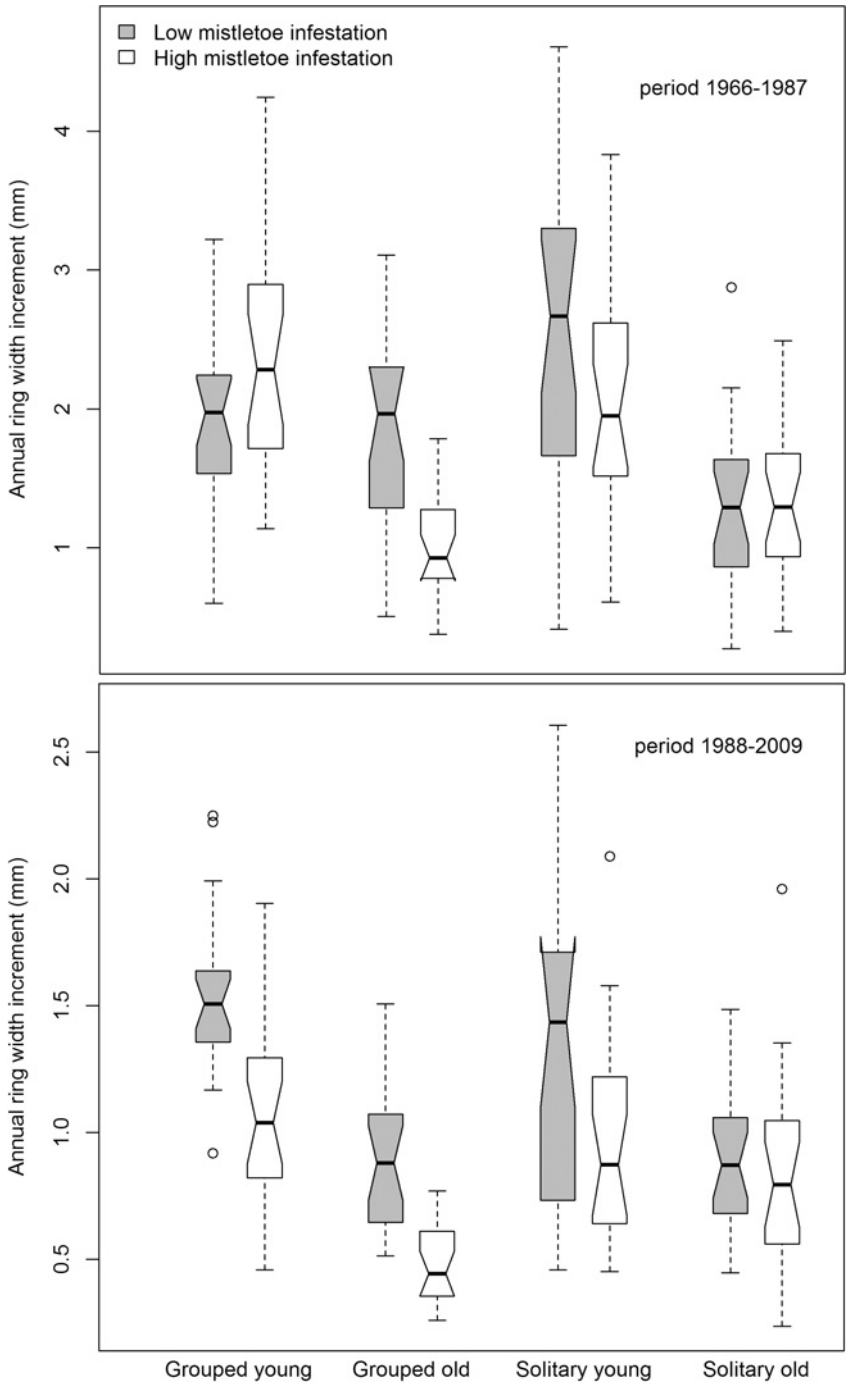


Fig. 1. – Comparison of the ring widths recorded in eight different categories of oak trees over two periods, 1966–1987 and 1988–2009. Boxes represent 25–75% of the values, bands near the middle of the box are the medians, whiskers indicate the 1.5 interquartile range and dots are outliers. If the notches in the boxes of two groups do not overlap this is strong evidence that the medians of these groups differ significantly.

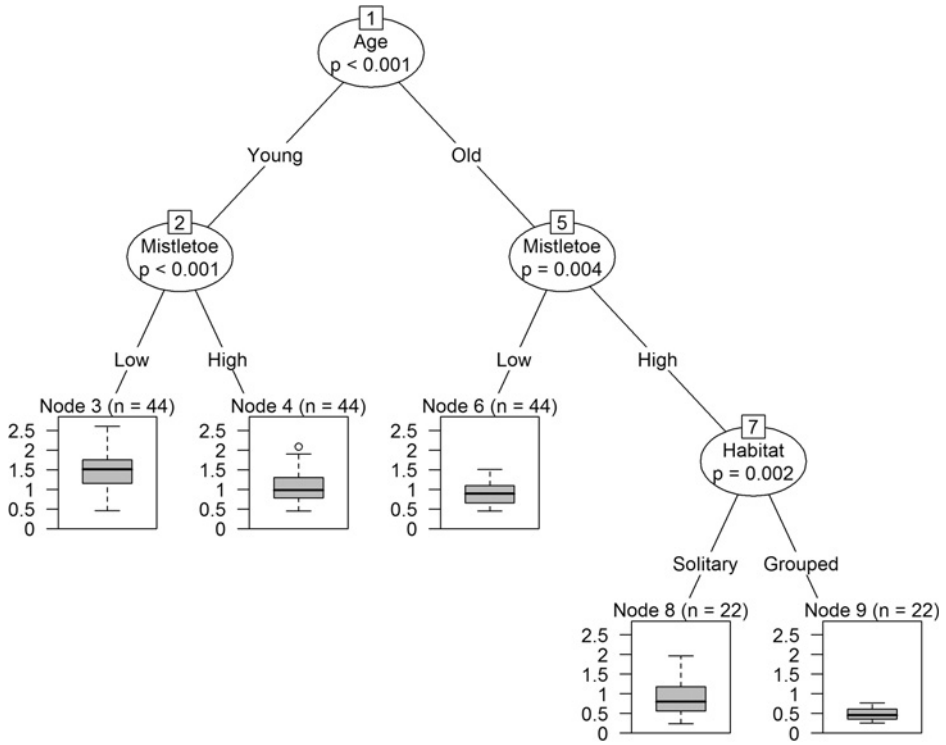


Fig. 2. – Conditional inference trees showing a significant effect of all three factors (age, habitat, mistletoe) on growth increments recorded in the period 1988–2009. The highest increments were recorded for young LMI trees, followed by young HMI trees and old LMI oaks; the smallest increments were recorded for old HMI oaks growing in groups (significant effect of competition). In each split of the tree, all predictors are tested and the one that best discriminates between thinner and wider increments is selected. Each split of the tree is described by the factors associated with the split (ovals), the permutation-based significance of the split (P-value) (ovals) and the level at which the split occurs (line between ovals and boxes). The number of years (n) is given at each terminal node (box-and-whisker plot).

Growth–climate correlation analysis

The response function analysis for the whole growth period reveals common climate signals for different chronologies and some specific features (Electronic Appendix 8). A negative growth response of latewood width to June T was recorded in all chronologies and compared with grouped trees, solitary trees reacted negatively to April P. Moving correlations for shorter intervals were much more informative than analyses of the whole growth period (Fig. 3). This revealed different growth–climate responses for solitary and grouped oaks and also much stronger climate relationships for HMI oaks. Latewood growth of mistletoe infested oaks responded negatively to high June T, particularly during the drier and warmer last two decades, whereas the responses of LMI oaks were weak and discontinuous. The chronology of grouped old HMI trees positively correlated with July P for the whole period, while in the other groups this relationship was missing or found only sporadically.

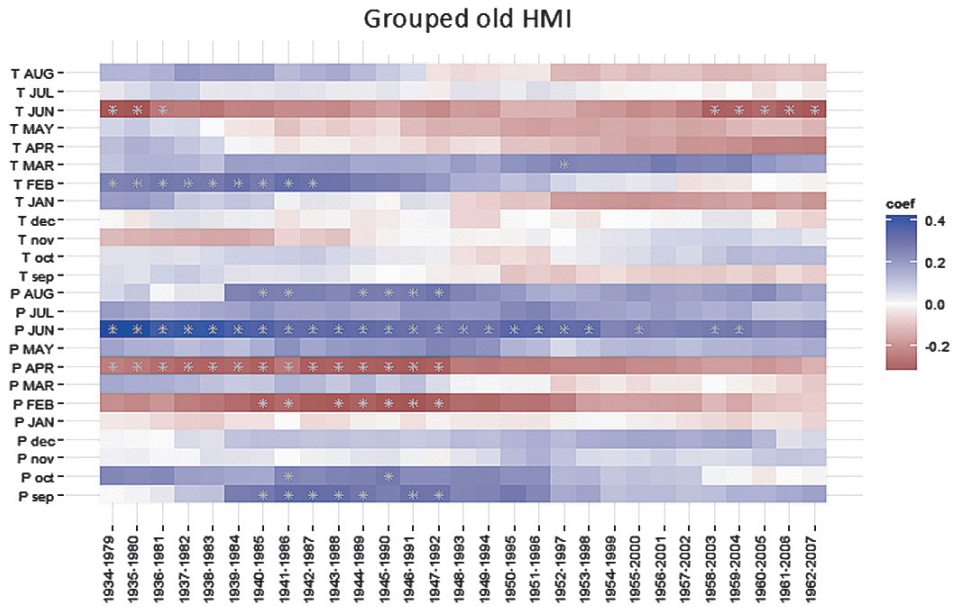
Assessing non-linear tree responses to climate using conditional inference trees

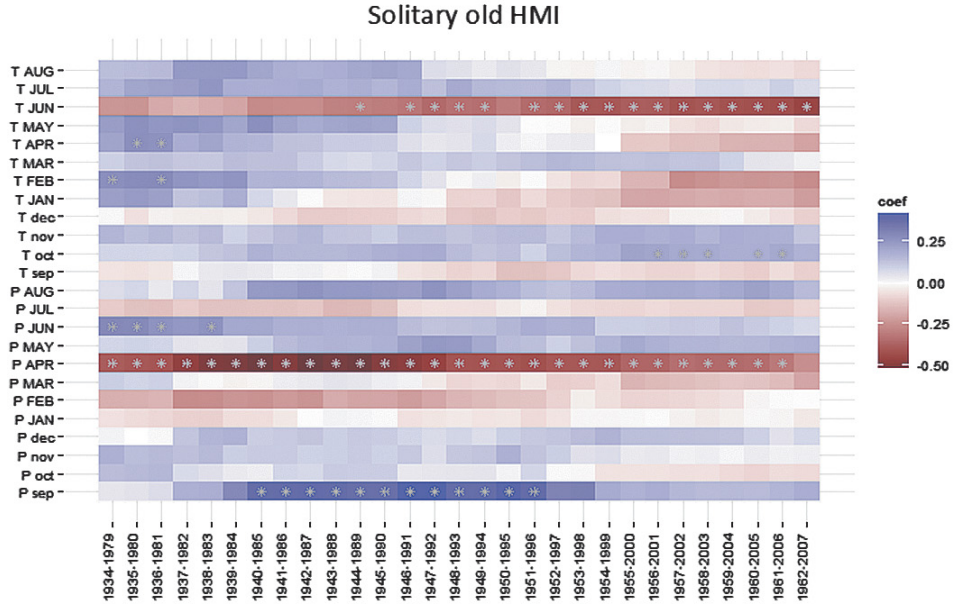
When compared to methods based on linear responses, the regression trees provided more comprehensive information about climate–growth relations (Figs 4 and 5). June T was the most important factor for HMI oaks, whereas May or April P was more important for LMI oaks (Electronic Appendices 9–10). The growth recorded for old HMI oaks in groups was significantly greater when mean June T < 18.4 °C, April P < 62 mm and March T > 3.3 °C. Similarly, solitary old HMI oaks grew more when June T < 18.6 °C, April P < 58 mm and August P > 39 mm. The maximum growth of young HMI oaks in groups was recorded when June T was lower (<16.6 °C) than that associated with the maximum growth recorded for old HMI oaks growing in groups. In years with warmer Junes (> 16.6 °C), the growth of young HMI oaks growing in groups was significantly greater when the prior December P was > 37 mm, March T > 3.8 °C and May T < 14.8 °C. For the young LMI oaks growing in groups, the best growth was recorded when May P > 50 mm and prior September P > 79 mm; in years with a dry May, growth was greater when July P > 81 mm and February P > 55 mm. The solitary young LMI oaks grew most when April P was < 62 mm, and prior September P > 47 mm and November P > 49 mm.

Dendrometer records of variations in intra-annual growth

The seasonal changes in growth recorded by the belt dendrometers revealed significant differences between the three individuals studied, with the greatest annual increment recorded for the solitary LMI oak, followed by the LMI oak growing in a group and solitary HMI trees. The annual variation in radial growth (Fig. 6) showed a typical pattern of spring swelling due to rehydration followed by a May–June period of fast growth, then slow growth from July to mid August associated with the prevailing high air T and lowest rainfall and soil moisture contents (Fig. 7A, B). The second period of active growth from mid August to the end of October was followed by a dormant period during which a slight winter shrinkage was recorded due to frost desiccation. During the four months of most active growth from May to August, there were 49, 55 and 62 days in 2012 and 52, 69 and 81 days in 2013 with positive net daily increments (ΔR) in the solitary HMI, solitary LMI and the LMI tree growing with other trees, respectively (Fig. 7G). Fewer days with a positive ΔR was recorded for the solitary LMI oak but it grew faster (higher ΔR values due to longer expansion phase) than the LMI tree growing with other trees (Fig. 7C, E). The growth of the solitary HMI oak was interrupted during the warmest July–August period when stem shrinkage occurred due to desiccation (Figs 7 and 8), while the two other LMI oaks continued growing even during the warmest part of growing season. Greater fluctuations with a more definite minimum and variation in radial growth were recorded for solitary oaks, for which the duration of the contraction phase was also longer, especially for the solitary HMI oak (Electronic Appendix 11).

The maximum daily shrinkage (MDS) and net increment (ΔR) were positively correlated with the duration of the contraction (DC) and stem radius increment (SRI) phases, respectively (Table 2 and Electronic Appendices 12–20). When the SRI increased, ΔR increased proportionally in all three individuals (no significant differences in the regression slopes), with the highest mean growth rate recorded for the solitary LMI oak and the lowest for the LMI oak growing with other oaks (significant differences in the regression intercepts). Both ΔR and SRI were negatively correlated with mean daily T (all three oaks)


Grouped old HMI
T AUG
T JUL
T JUN
T MAY
T APR
T MAR
T FEB
T JAN
T dec
T nov
T oct
T sep
P AUG
P JUL
P JUN
P MAY
P APR
P MAR
P FEB
P JAN
P dec
P nov
P oct
P sep
1934-1979
1935-1980
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1955-2000
1956-2001
1957-2002
1958-2003
1959-2004
1960-2005
1961-2006
1962-2007
coef
0.4
0.2
0.0
-0.2


Solitary old HMI
T AUG
T JUL
T JUN
T MAY
T APR
T MAR
T FEB
T JAN
T dec
T nov
T oct
T sep
P AUG
P JUL
P JUN
P MAY
P APR
P MAR
P FEB
P JAN
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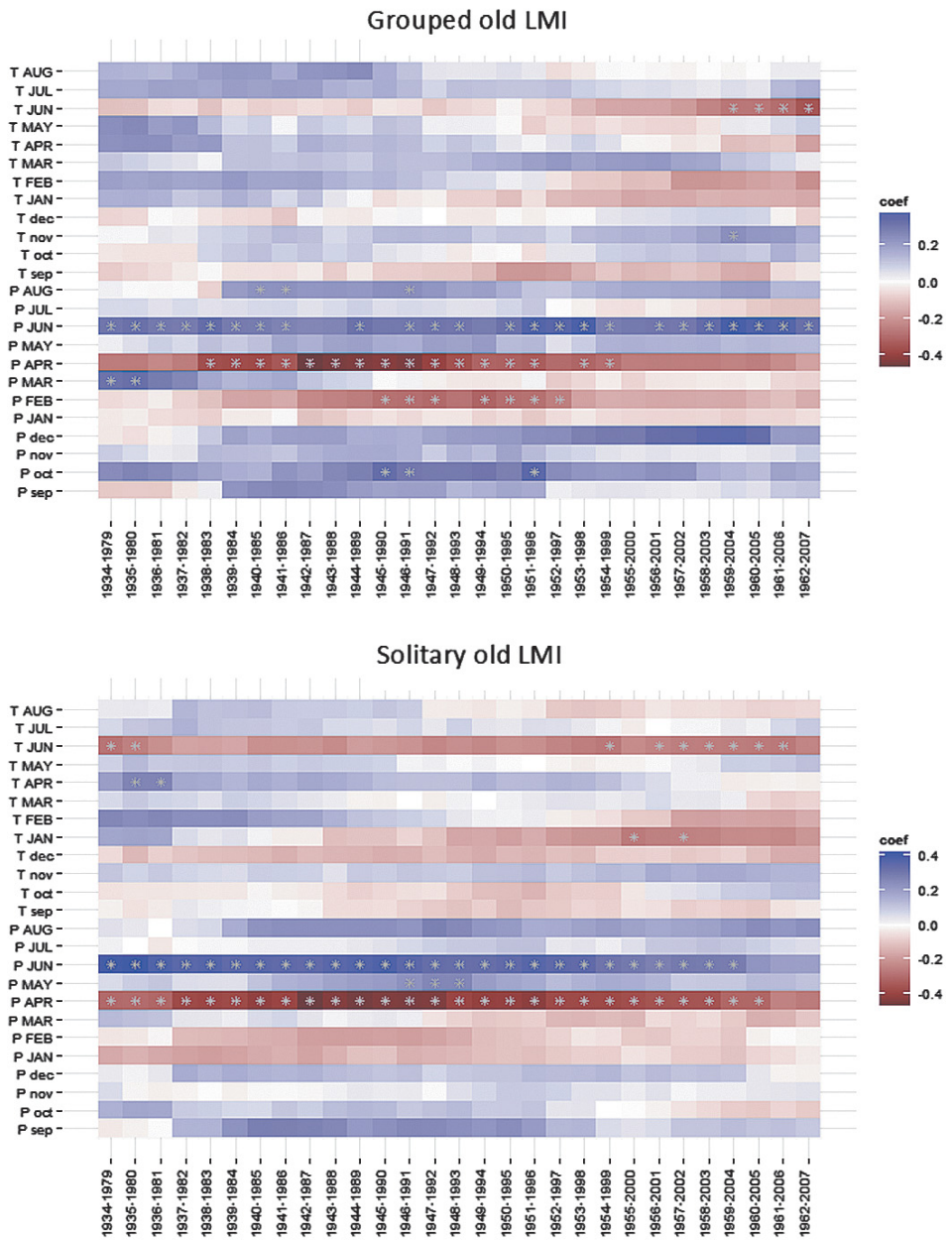


Fig. 3. – Bootstrapped moving correlation function relating latewood growth to the temperature and rainfall from the previous September to current August. The moving correlation is carried out in windows of 45 years, over the period 1934–2007. The blue areas correspond to the positive values and the red areas to negative ones. Significant correlations are denoted by the asterisks.

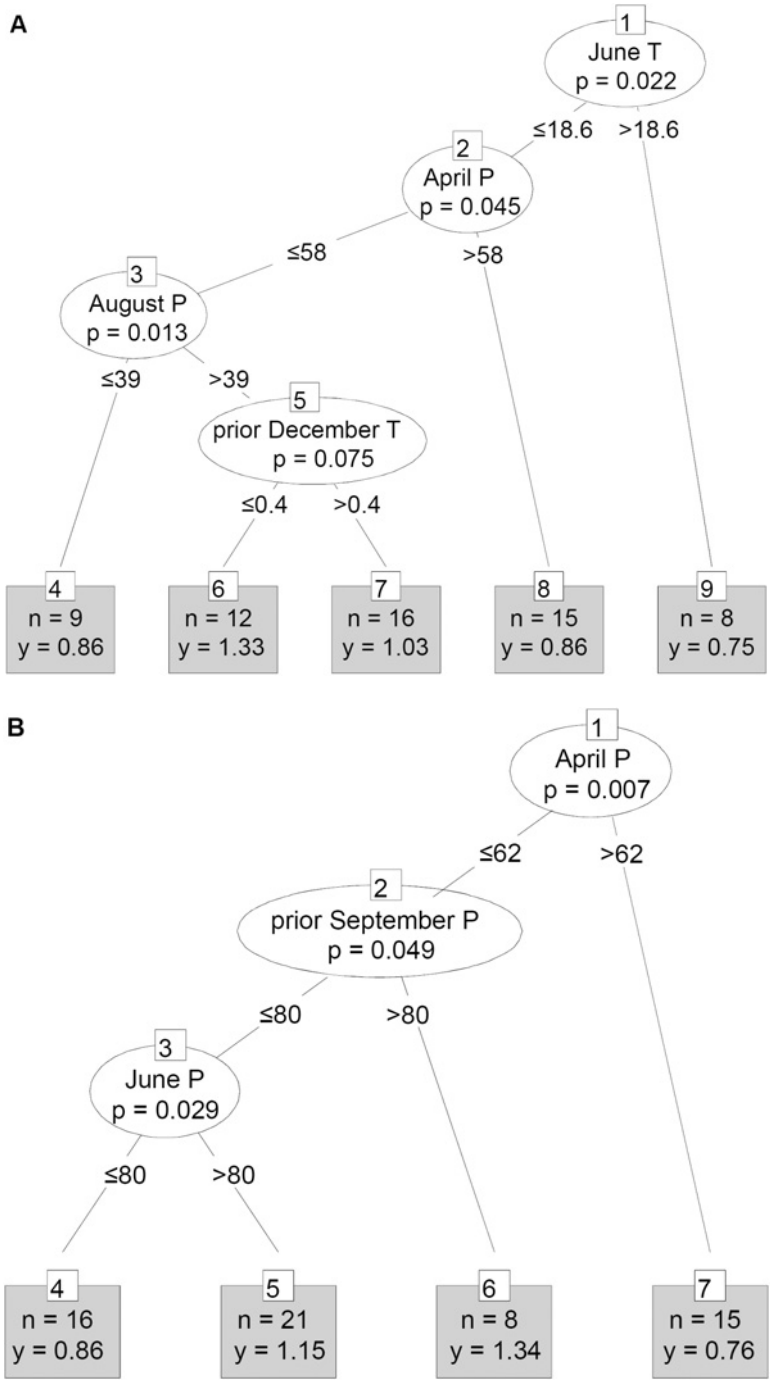


Fig. 4. – The conditional inference trees showing latewood growth–climate relationships for solitary old oaks with different levels of mistletoe infestation (A – high, B – low). In each split of the tree, all monthly climate predictors are tested and the one that best discriminates differences in growth is selected. The procedure goes on until no predictor significantly discriminates growth. The response variable (y) is the latewood growth indices from residual chronologies. Each split of the tree is described by the climatic factor associated with the split (ovals), the permutation-based significance of the split (P-value) (ovals) and the threshold values at which the split occurs. The number of years (n) and mean latewood index (y) is given at each terminal node (box).

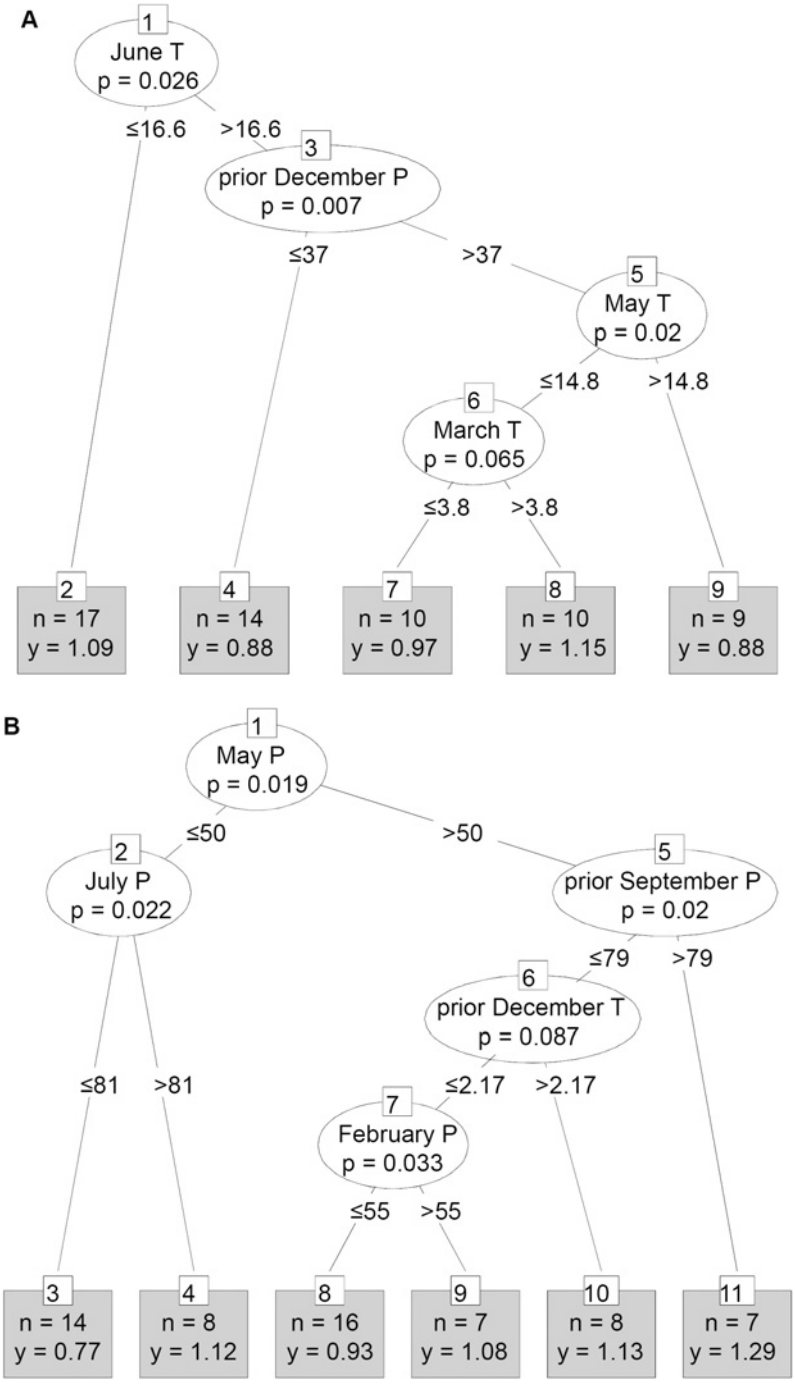


Fig. 5. – Assessing non-linear tree responses to climate using conditional inference trees for young oaks growing in groups with two different levels of mistletoe infestation (A – high, B – low). See Fig. 4 for details.

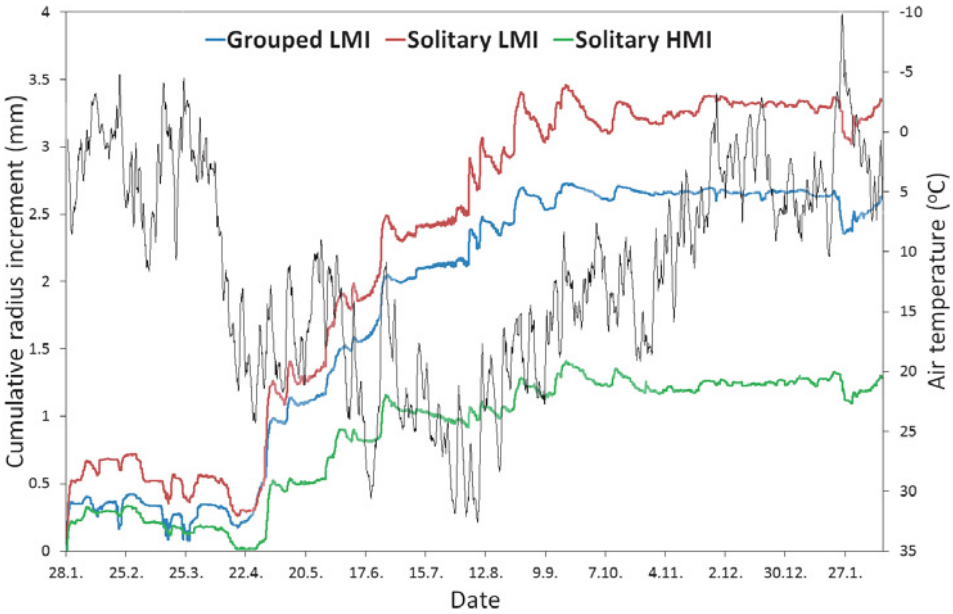
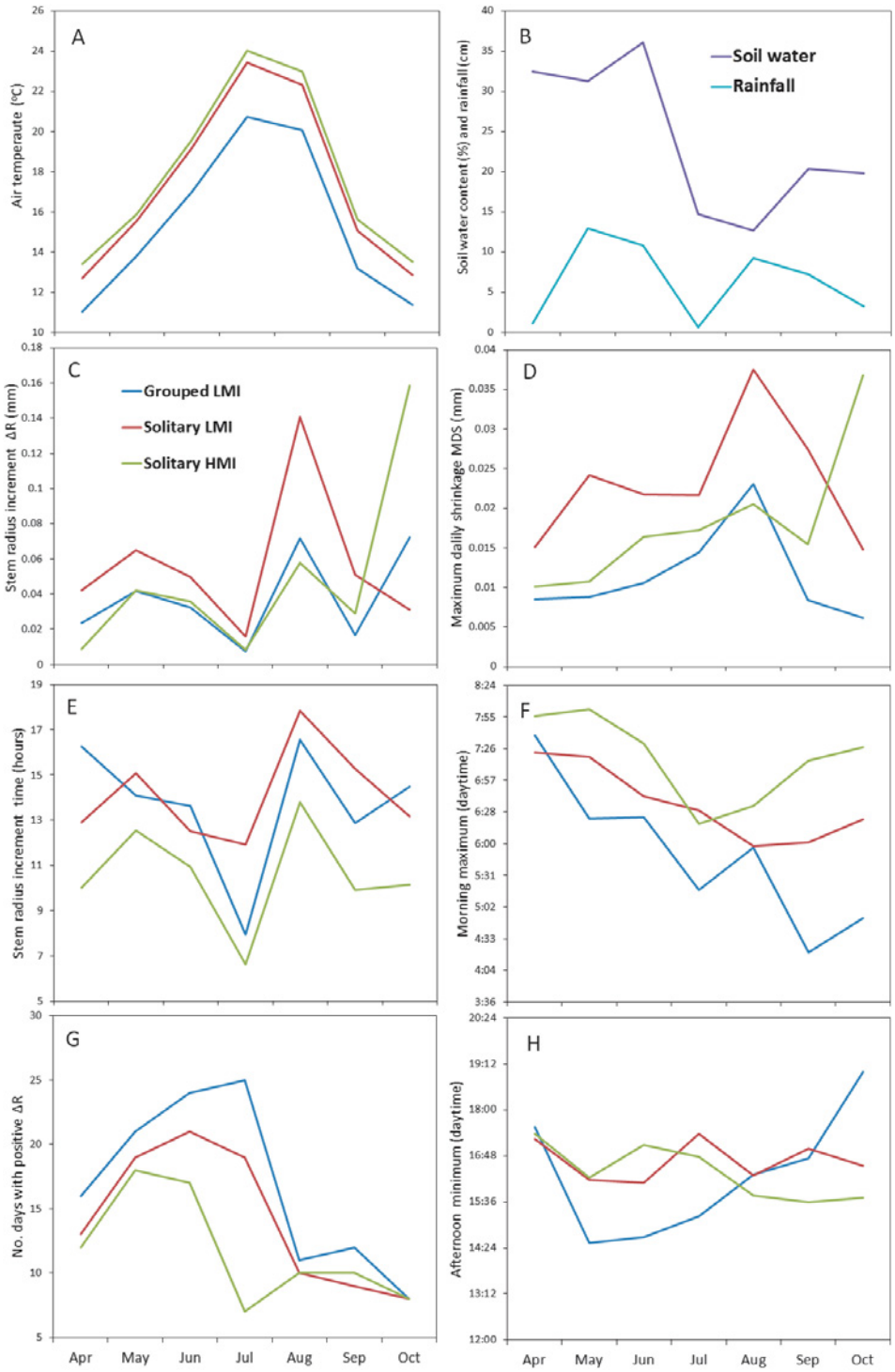


Fig. 6. – Seasonal radial increments and air temperatures monitored using a belt dendrometer for three oaks growing either solitary or in groups with either a low or high mistletoe infestation in 2013.

and positively with mean soil water content and daily rainfall sum (significantly only for the LMI oak growing with other oaks). After controlling for the effect of the duration of the SRI phase on ΔR using multivariate regressions, daily T had no significant effect on ΔR (Table 2). Hence, the negative correlations between ΔR and T are due to the negative effect of T on the duration of the SRI phase. The amplitude of the daily cycle in terms of MDS and DC, was highest for the solitary LMI oak and lowest for the solitary HMI oak, and for all the trees studied decreased with soil water content and increased with mean T. Moving correlations (Electronic Appendices 21) support these conclusions, but also indicate that the relative importance of particular climatic variables changes during the course of a day and a growing season. There were stronger correlations between ΔR and soil water content between 06.00–12.00 hours in two periods, during earlywood formation (beginning of May) and the end of the growing season in September and October. Temperature played a more important role in the middle of the growing season (June–July), with a particularly strong negative correlation recorded between 12.00 and 18.00 hours.

Fig. 7. – Time-series of meteorological data and variations in stem diameter of three oaks from April to October 2013. Meteorological data included (A) air temperature, (B) rainfall and soil water content. Variation in radial growth of the trunks was expressed in terms of (C) mean daily stem radius increment (ΔR) for days with positive Rmax cycle, (D) maximum daily shrinkage (MDS), (E) duration of stem radius increment phase (SRI), (F) morning maximum: onset of contraction (shrinking) phase, (G) number of days with positive ΔR, and (H) afternoon minimum: onset of expansion (swelling) phase. ▶


A
Air temperaute (°C)
B
Soil water content (%) and rainfall (cm)
Soil water
Rainfall
C
Stem radius increment ΔR (mm)
Grouped LMI
Solitary LMI
Solitary HMI
D
Maximum dalily shrinkage MDS (mm)
E
Stem radius increment time (hours)
F
Morning maximum (daytime)
G
No. days with positive ΔR
H
Afternoon minimum (daytime)
Apr
May
Jun
Jul
Aug
Sep
Oct

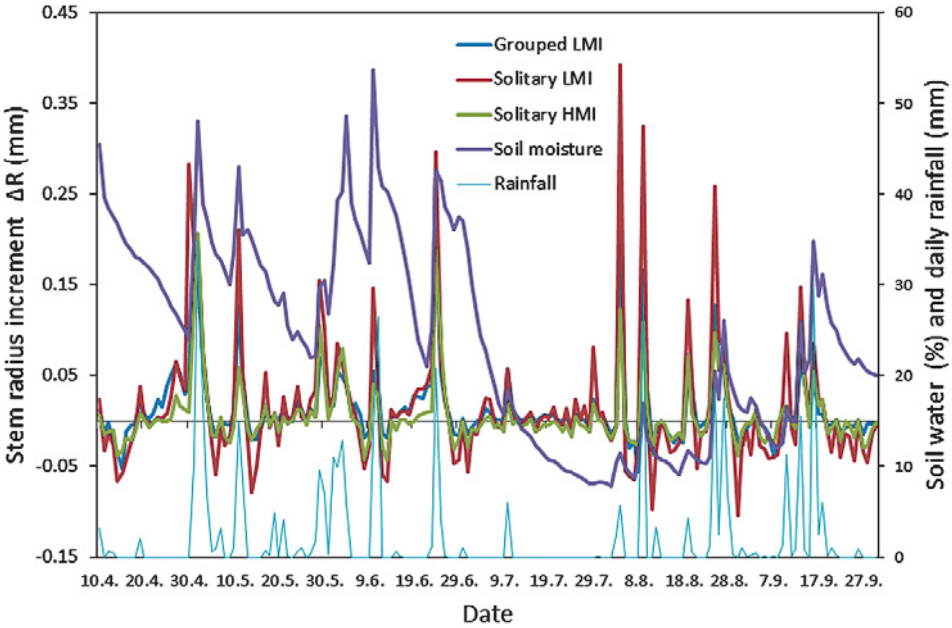


Fig. 8. – The net daily increments are positively correlated with the sum of daily rainfall and soil water content, and negatively with mean air temperature. Data for the 2013 growing season, shown for grouped and solitary oaks with low (LMI) and high (HMI) mistletoe infestation.

Table 2. – Relationships between daily net stem radius increment (ΔR) and the duration of the stem radius increment phase (SRI), maximum daily shrinkage (MDS) and the duration of the contraction phase (DC), and mean daily soil water content (SM) and mean daily air temperature (T) for three oaks (solitary with low or high mistletoe infestations and grouped with low mistletoe infestation). The data were calculated from diurnal cycles recorded in the period April–October 2013. Adjusted R-squared values (for more details see Electronic Appendices 14–21), and significance values of the regression tests (ns: nonsignificant, [a] $P < 0.1$, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$) are shown.

Parameter	Grouped LMI	Solitary LMI	Solitary HMI
ΔR~SRI	+0.18***	+0.18***	+0.18***
MDS~DC	+0.42***	+0.56***	+0.36***
ΔR~SM	+0.13***	+0.08**	+0.06[a]
ΔR~T	–0.08***	–0.08**	–0.05*
SRI~SM	+0.12***	ns	ns
SRI~T	–0.14***	–0.08**	–0.20***
MDS~SM	–0.13***	–0.04**	–0.05**
MDS~T	+0.13***	+0.05**	+0.11***
ΔR~SM+Error(SRI)	ns	+0.04*	ns
ΔR~T+Error(SRI)	ns	ns	ns

Discussion

It is proposed that oak growth decline is a result of the synergistic effects of several internal and external drivers (Manion 1981, Doležal et al. 2010, Rozas 2015). This study shows that oak decline is associated with mistletoe infestation, competition from neighbouring trees, climate warming and frequent droughts, which are associated with a decrease in wood formation. These effects were most marked during the warmer and drier 1988–2009 period. Of the eight categories of pedunculate oaks (*Quercus robur*) studied, old trees infested with mistletoe and subject to competition from neighbouring trees grew least and were most prone to extreme climatic events. Trouvé et al. (2014) report that poor growth in oaks is associated with high summer soil water deficits, especially if the roots of the trees have to compete with the roots of other trees for water.

Annual variation in radial growth

This study shows that the negative effects of climatic factors include a combination of dry or cold winters and springs, which result in little snow melt and a subsequent water shortage during earlywood formation. If this is followed by a cool and wet April, which delays the onset of latewood growth, and a hot and dry May and June, which reduces latewood formation, narrow tree rings are formed. Severe summer droughts may result in poorly acclimatized oaks becoming more sensitive to low winter temperatures and their roots being damaged by frosts (Helama et al. 2009). Thomas & Ahlers (1999) report that droughts the previous summer diminish bark frost hardiness in pedunculate oaks, thereby increasing the risk of frost damage. This predisposition, however, is site- and age-specific. Helama et al. (2009) document that due to summer droughts in Finland, the growth of poorly acclimatized pedunculate oaks is sensitive to low February temperatures and frost damage to roots; however, this response was not recorded in healthy trees growing on less water-limited sites with deep soils. The prolonged periods of unfavourable conditions for growth, such as those in the 1990s, caused oak trees to become more prone to infestation with mistletoe (*Loranthus europaeus*) (Thomas et al. 2002). Mistletoe spreads and grows relatively slowly and is rarely considered an immediate threat to tree health, with healthy trees able to tolerate a few mistletoe plants with little obvious harmful effect. Trees that are heavily infested with mistletoe became less vigorous, stunted and are killed if subjected to additional stress from drought, extreme temperatures, root damage, insect infestation or disease.

The positive association of the width of latewood in annual rings with summer precipitation and negative association with temperature in our dataset indicates that growth is favoured by cool, humid, and therefore relatively moist weather during the period of active growth, as in other parts of the range of pedunculate oak in Europe (Pilcher & Gray 1982, Bednarz & Ptak 1990, Lebourgeois et al. 2004, Rozas 2005, Čufar et al. 2008, Drobyshev et al. 2008, Doležal et al. 2010, Popa et al. 2013, Sohar et al. 2014b). Even if all oak trees respond positively to a wet May–June and are thus affected by similar climatic factors, our data indicates certain habitat dependent differences (Tyree & Cochard 1996). In particular, solitary oaks were limited by rainy/cool Aprils delaying the onset of the growing season, unlike the oaks growing in groups. The negative effect of cool April weather was recorded for both young and old solitary oaks. The site studied is on a windy west-facing slope on impermeable calcareous clay and sandstone bedrock, which results

in surface runoff being rapid and extreme climatic situations occurring regularly. Moreover, most of the area is subject to water erosion and landslides are a common phenomenon (Jongepierová 2008). Hence, solitary oaks may presumably suffer more from extreme spring conditions than those growing in close stands of groups of trees which have a more favourable microclimate. Between-habitat comparison of in-situ climate records revealed a 2.4 °C higher mean April temperature in groups of trees than that associated with solitary trees.The early spring advantage of growing in a group of trees, however, can quickly become disadvantageous during a hot summer (mean July temperature is 3.3 °C higher inside than outside a wood) as trees growing in groups, unlike solitary trees, must compete for water and nutrients with their neighbours; this, combined with old age and high infestation with mistletoe, is associated with poor latewood production. The habitat dependent differences in competition for resources may account for the positive association between the growth of oaks growing in groups and July precipitation, but this relationship was not recorded for solitary individuals.

This study combines several recent innovations in the modelling of tree growth and climate (Zang & Biondi 2015). The evaluation of short climate signals using moving correlations is a useful tool when tree growth–climate relations are not constant over time or may even reverse (Doležal et al. 2016). In such cases, the analysis of the whole growth period spanning several decades or centuries may not provide any meaningful information due to the mixing of opposite effects. This is seen in this study in the positive latewood responses to high February temperature during the colder periods of the first half of the last century that became neutral or negative during the second half. Also, positive latewood responses to high April–May temperature during the colder 1930s–1940s changed to negative during the warmer 1900s–2000s, which reflected spring warming and a prolonged growing season. The effects of summer heat waves and associated droughts on oak growth, the frequency of which has increased due to the increase in warming since the 1990s, appears to have been made worse by a mistletoe outbreak. The spread of mistletoe may also be associated with socioeconomic changes during the 20th century that have led to a reduction in traditional land-use practices. European oak forests have become considerably denser and even-aged during the last 50–70 years due to the policy of increasing timber production, availability of sources of fuel other than wood and the concurrent abandonment of such traditional management techniques as coppicing and woodland pasturing (Altman et al. 2013). Progressive conversion to high-forest management, accompanied by canopy closure and uniformity of forest environments, particularly in lowland oakwoods, has led to a poor recruitment of oaks and may have also favoured the spread of mistletoe from tree to tree.

This study showed that within the same age and habitat category, trees heavily infested with mistletoe grew significantly slower and were limited by different climatic factors than healthy oaks. Most of the information about this difference was provided by the conditional inference trees. The use of this novel method in dendroclimatology provided a more complete picture of the many constraning climatic factors, their interactions and treshold values. It clearly demonstrated that trees with a high mistletoe infection are primarely controlled by high June–July temperature, while the less infected trees are more controlled by precipitation, mostly in May. During the dry and hot June–July period, when most of the latewood cells are produced, the otherwise independent stomatal control of the host and hemiparasite become linked because transpiration demands may

exceed supply. According to Glatzel & Geils (2009), mistletoe needs to be able to tolerate a more negative water potential than the host in order to maintain a flux gradient and avoid stomatal closure and wilting. This is ensured by the succulent leaves that enhance water storage and allow mistletoes to rehydrate before their hosts rehydrate. Mistletoe infections may therefore disrupt the host stomatal control system, causing early and oscillating closure of host stomata, thereby diminishing host photosynthetic gain and latewood formation. When the stomatal control system is not disrupted by mistletoe, healthy oaks can easily cope with summer heat by transpiration cooling and their latewood formation seems to be controlled by the speed of earlywood formation in May, which is determined by a sufficient supply of water rather than by temperature, which stays within the optimal range of 10–20 °C.

Dendrometer records of variations in intra-annual growth

Dendrometer records support the results of the study of tree rings. Net daily increments increased with soil moisture and decreased with high daytime temperature. These factors have, however, an indirect effect, which is modulated by the duration of the growth phase. Similarly, Deslauriers et al. (2007) conclude that the negative correlation between ΔR and air temperature is caused by the effect of temperature on phase duration and does not correspond, on a daily scale, with a direct physiological effect on tree growth mediated by an effect on their metabolic activity. Hence, the oaks studied differed in the duration and not the speed of their growth. Infested oaks have smaller increments because of a shorter period of growth rather than an altered carbon metabolism (Daudet et al. 2005, Zweifel et al. 2006). Solitary oaks have higher MDS (daily amplitudes) than oaks growing in groups due to the greater daily fluctuations in temperature in open landscapes than in enclosed woods, and hence are more sensitive to high summer temperature. This results in a smaller number of days with a positive ΔR compared to oaks growing groups. However, when temperature and moisture conditions are optimal (soil moisture > 20%, mean daily temperature 10–20 °C), solitary oaks grow for longer than oaks growing in groups, which compete for resources with neighbours and hence their growth is more limited by the availability of water than in solitary trees. This results in a strong dependency of ΔR or the duration of growth of oaks growing in groups on soil moisture; a pattern not recorded for solitary oaks. The longer duration of growth compensate for fewer days of active growth and results in the larger total annual increments recorded for solitary oaks than those growing in groups.

The net daily increments are a function of the durations of the contraction and expansion phases, which change during the course of a growing season depending on the availability of soil moisture and temperature stress. Oaks growing in groups, which are more limited by soil water deficit, have a shorter contraction phase than solitary oaks as they are able to fully rehydrate early in the morning (4:30 to 6:30) and close their stomata early in the afternoon (14:30 to 15:30) to avoid late-afternoon water loss. At the beginning of the growing season in May and June when the soil is wet (about 30% water content), MDS and radius contraction phases are shorter during regular cycles, which implies that the water loss to the atmosphere controlled by temperature was fully compensated by root absorption during the whole day. In the later part of the growing season, in July and August, when the soil is dry (less than 15% water content), stem contraction is recorded

from early morning onwards. When temperature was high and soil moisture low, water demand exceeded uptake and the stem radius decreased. Similar shifts in maximum onset and in the amplitude towards higher water demands (higher temperature, more sunshine) and drier soil conditions (less precipitation) are reported for various species of trees by King et al. (2013).

Our novel approach of using moving correlations of the dendrometer-derived increment data revealed how the formation of early- and latewood are dependent on water availability and temperature experienced during the course of an entire growing season. During the two peaks of growth (May–June and late August–September) temperature was mainly in the optimal range of 10–20 °C, which is below the critical temperature of 18–19 °C proposed by the conditional inference tree model for optimal latewood formation. At the beginning of active growth in early May, when earlywood vessels are developing, conductive tissues are not fully saturated with water and hence on warm days with mean temperature > 20 °C, overheated trees cannot effectively cool down by transpiration. The importance of water supply for early growth is illustrated by a strong relationship between net daily increments and daily rainfall in May. Once xylem conduits are fully saturated in June and July, daily increments are determined by high temperature and associated drought, while later in the season in August and September, when mean daily temperature drops below 20 °C, the importance of soil moisture for growth is relatively high. Obviously, the negative effect of high temperature on radial increments is related to the water balance. The high rate of transpiration due to high temperature may lead to a water deficit in plant tissues, which inhibits cambial growth by a complex process that includes a lowering of the turgor pressure in cells and changes in carbon balance (Sevanto et al. 2003, Daudet et al. 2005, Steppe et al. 2006, Zweifel et al. 2006, De Schepper & Steppe 2010). High soil moisture combined with optimum temperature has a positive effect on the rate of cell division (Körner 2012), xylem element enlargement (Panyushkina et al. 2003, Fonti et al. 2007, Sterck et al. 2008) and carbon investment in structural growth (Shi et al. 2008, Hoch & Körner 2012). The importance of water supply for growth is illustrated by a strong relationship between radial increments and rainfall (Downes et al. 1999), soil water content (Oberhuber et al. 2014) and vapour pressure deficit (Urrutia-Jalabert et al. 2015) reported in numerous studies in temperate (Oberhuber & Gruber 2010, Köcher et al. 2012), boreal (Tardif et al. 2001, Deslauriers et al. 2003) and montane (Oberhuber et al. 2014) regions.

Conclusions

This is a first comparative dendrochronological study of the effect of tree age, competition and mistletoe infestation on the growth of pedunculate oak and its association with differences in both annual and intra-annual climate in the warm south-eastern part of the Czech Republic, a drought-prone area where oaks die prematurely. Extreme climatic events such as summer drought, in association with mistletoe infestation, are hypothesized as factors responsible for oak decline. We tested this by comparing latewood widths of eight categories of oaks with the monthly climatic data recorded in the period 1904–2009, using a combination of linear methods (response function, moving correlations) and non-linear regression trees, a novel method in dendroclimatology that provides

a more complete picture of the constraining factors than traditional linear methods. As an alternative to long-term records of tree-ring widths, we also continuously monitored intra-annual growth during the vegetative period using automatic belt dendrometers.

Moving correlations between net daily increments and in-situ measured soil moisture and air temperatures provided detailed information on a tree's reaction to the whole season's climatic conditions. All approaches clearly showed that a shortage of water due to low rainfall and high temperature during the period of latewood formation (May–October) negatively influences latewood growth and hence the total annual growth increment. The effect of adverse climatic conditions was reinforced by mistletoe infestations and competition from neighbouring trees. The increase in summer temperatures and frequent occurrence of severe summer droughts over the course of the last three decades, in combintaion with an increasing rate of mistletoe infestation, negatively affected radial stem growth of oaks in the White Carpathians and may have significantly contributed to their recent decline.

See www.preslia.cz for Electronic Appendices 1–21

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Souhrn

Nedostatek srážek a rostoucí letní teploty během posledních tří dekád mohou mít negativní vliv na růst dubu letního (*Quercus robur*) a významně přispívat k jeho předčasnému odumírání. Dlouhá perioda nepříznivých klimatických podmínek může dále způsobit, že oslabené duby jsou náchylnější k infekci houbovými chorobami a ochmetem, což vede k dalšímu oslabení nebo smrti. Na základě rozsáhlého odběru vzorků z dubů rostoucích solitérně nebo v malých lesících v savanovité krajině druhově bohatých luk Bílých Karpat, nejzápadnějšího výběžku Karpat v jihovýchodní části České republiky, jsme chtěli zjistit, jak je šířkový přírůst kmenů ovlivněn klimatickými výkyvy v interakci s kompeticí sousedů a napadením ochmetem. Celkově jsme porovnali radiální růst osmi skupin dubů lišících se věkem (mladší nebo starší než 60 let), kompeticí (solitérní oproti seskupeným) a napadením ochmetem (silně zamořené oproti zdravým jedincům). Vliv klimatu byl hodnocen srovnáním šířky letokruhů s klimatickými daty za období 1904–2009. Kromě dlouhodobé odezvy jsme zkoumali denní růstové změny pomocí dendrometrů během dvou sezón, 2012 a 2013. Data byla analyzována použitím kombinace tradičních dendroklimatických metod (mnohonásobná regrese, posuvné korelace, analýza extrémních letokruhů) s nelineárními regresními stromy. Růst dubů ovlivňují (1) suché a chladné zimy, které mají za následek poškození kořenového systému a nedostatek vody v létě, (2) chladný a vlhký březen a duben, který brzdí nástup tvorby jarního dřeva a (3) teplé a suché letní období, které redukuje formování letního dřeva. Optimální přírůsty nastávají pokud jsou únorové srážkové úhrny > 55 mm, průměrné březnové teploty > 3,3 °C, dubnové srážkové úhrny < 60 mm, květnové srážkové úhrny > 50 mm, červnové teploty < 19 °C, a srpnové srážkové úhrny > 40 mm. Šířka letního dřeva a tím i celkový roční přírůst klesá s věkem stromů, napadením ochmetem a kompeticí sousedních stromů. Tyto faktory jsou zodpovědné za rozdílné růstové odpovědi na změny klimatu. Deficit vodní bilance jako následek nízkých srážek a vysoké teploty během června a července vede k negativní růstové bilanci u ochmetem napadených dubů, omezenému formování letního dřeva a tím i nižšímu celkovému ročnímu přírůstku. Růst zdravých dubů je řízen především květnovými srážkami, které určují, jak rychle je dokončena tvorba jarního dřeva, a tedy jak bude dlouhé období tvorby letního dřeva. Seskupené stromy čelící konkurenci o vodu jsou náchylnější k suchu během června a července, zároveň jsou však méně citlivé k negativním vlivům studeného jarního počasí. Opačně je tomu u solitérních dubů, které jsou v otevřené krajině vystavené většímu

kolísání teplot, což vede k menšímu počtu dní s pozitivní růstovou bilancí (ΔR). Nicméně v případě optimálních podmínek (půdní vlhkost > 20%, denní teploty v rozmezí 10–20 °C) mají solitérní duby delší trvání denní růstové fáze, což vede k celkově většímu ročnímu přírůstku než u seskupených dubů. Záznamy z dendrometrů tedy ukazují, že rozdíly v denních přírůstech jsou primárně dány délkou trvání fáze růstu, nikoli změnou rychlosti růstu. Napadené duby mají menší ΔR a celkový roční přírůstek kvůli kratší době růstu nikoli pozměněnné metabolické aktivitě. Tato studie ukázala, že pokles růstu dubů je spojen s ochmetem, kompeticí sousedních stromů a dlouhodobějším vlivem nepříznivých klimatických podmínek. Naše výsledky podporují představu o klíčové roli klimatických změn a lokálních biotických interakcí v procesu vedoucímu k odumírání vysokého počtu dubů na bělokarpatských loukách.

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