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Physiological and growth response of *Quercus robur* in Slovenia

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Abstract: Pedunculate oak (*Quercus robur* L.) forests in Slovenia are experiencing widespread mortality. Changes in lowlands reflect in decline of complete forest complexes, high mortality, uneven stand structure and associated forest regeneration problems. Prediction of the present-tree response in disturbed forest ecosystems may significantly contribute to better guideline policies for the silvicultural and forest management practice in the changing environment in both stressed and stable forest ecosystems. On pedunculate oak floodplain site two groups of vital and declining trees were selected according to the ICP methodology. During three consequent vegetation periods (2006, 2007 and 2008), ecophysiological response of trees in controlled conditions (maximal photosynthetic rates – A_{\max} , water conditions) were recorded and compared with radial growth (tree ring width, pointer years). Growth was compared with meteorological data from closest meteorological stations to recognize and define tree response to changing growing conditions in all groups. Significant differences in light response (A_{\max}) between declining and vital trees were observed as well as in water use efficiency (WUE) and in pre-dawn water potential (Ψ_{pd}). Beside the differences in tree-ring width, a significant difference in the year-to-year variability of tree-rings between both studied oak groups was confirmed. Vital oaks in floodplains responded positively to above average precipitation in May and June, while declining oaks with very narrow rings, usually consisting of only one row of vessels, responded negatively to above average temperature in March.

Additional key words: Pedunculate oak, growth, tree-ring width, photosynthesis, water stress, lowland forests, climate response

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Introduction

European oak forests represent important ecosystems as sources of high-quality wood and, since they grow in lowlands, very important wildlife habitats and biodiversity hot spots. Pedunculate oak (*Quercus robur* L.) forests in particular are experienc-

ing widespread mortality in Europe. High mortality rates have resulted in uneven age-class proportions and have reduced seedling regeneration, resulting in sustainability concerns. Oak mortality has occurred repeatedly during the past three centuries and became more pronounced in recent decades in Europe (Thomas et al. 2002) and North America (Allen et al.

2010). Although the cause of mortality is currently unknown, it has been associated with changes in water availability (Hämmerli and Stadler 1989; Levanič 1993; Cochard et al. 1996; Triboulot et al. 1996; Tyree and Cochard 1996; Čater 2003; Čater and Batič 2006), weather extremes and forest management choices (Harapin and Androić 1996). Many studies have also explained periodic oak decline as a consequence of climate extremes and pathogens (Führer 1992; Donaubaue 1995) or by the occurrence of *Phytophthora* fungi, although the primary pathogenicity remains unknown (Jung et al. 2000).

Slovenian lowland oak forests are experiencing clear impacts, particularly on sites which are under severe agricultural pressure (Wraber 1951). The proportion of adult forest stands is declining and sanitary cut increases because of physiological weakening and high oak mortality (Čater and Batič 2006). Recent studies suggest that reduction of natural area in lowland forests is in direct connection with agricultural activities and reduction of groundwater table (Levanič 1993; Čater and Levanič 2004). Changes in lowlands reflect in decline of complete complexes, high mortality and uneven stand structure with associated problems in natural regeneration.

Study and prediction of the present-tree response in disturbed forest ecosystems may significantly contribute to better guideline policies for the silvicultural and forest management practice in the changing environment in both stressed and stable forest ecosystems.

Main goal of the research was to evaluate status of the lowland oak stands, to prepare guidelines for management in changed environmental conditions and to predict their perspective from the ecological point of view.

Long-term changes in tree growth due to lowering underground water and climate were compared with ecophysiological measurements – photosynthesis, transpiration and water uptake in the crown of adult pedunculate oaks. The main objectives of our study were (1) to compare ecophysiological and growth response of adult trees of different vitality group, and (2) to recognize and define tree response to rapidly changing environmental conditions.

Material and Methods

Plot description

The study site was located in the forest district of Brežice, Slovenia, at pedunculate oak (*Quercus robur* L.) forest site in a floodplain area (45.8638°N, 15.4302°E). The stand is 2400 ha in area, located on flat terrain at 156 m elevation. The area experiences a continental climate with 1147 mm/year precipita-

tion, 58% of which falls during the period when oak foliage is present (April–September). The average yearly mean, maximum and minimum temperatures are 9.9, 15.1 and 5.3°C, respectively. The soil is deep, seasonally saturated and strongly gleyed (amphigleys) on the Pleistocene clay and loam. The plant community is classified as *Querco-robore carpinetum*, with the overstorey dominated by *Q. robur* and an understorey of hornbeam (*Carpinus betulus*). The stand is dominated by even-aged oaks that were 125–145 years old in the year of sampling (2006–08) with stand density of 250–300 trees/ha.

Six vital and six declining dominant trees per species according to the ICP methodology were selected for ecophysiological measurements. Additional 15 vital and 15 declining trees have been randomly selected for the analysis of tree-ring widths and study of tree's response to environmental changes. In total 21 vital and 21 declining trees were analysed for dendrochronological analysis. Trees were defined as vital if defoliation rate was below 50% of total potential crown foliage and declining with crown defoliation above 75%, according to the International Co-operative Programme on Forests methodology (ICP) (Anonymous 2006). Typical signs of dying oaks are dry branches, partially dead crowns and pale green to yellowish leaves at the end of branches. All sampled trees were dominant – class 2 after Assman's classification (Kramer 1988) without visible damage of the stem or crown. Study plots have been fenced (50×50 m) and observed during three consequent vegetation periods (2006, 2007 and 2008).

Ecophysiological measurements

Photosynthesis was measured with the LI-6400 portable system. At least three sun canopy locations per tree were used for one measurement, located in the upper third of the tree-crown height on every plot at a constant temperature of the measurement block (20°C), a CO₂ concentration of 350 μmol/l, flow 500 μmol/s and different light intensities: 0, 50, 250, 600 and 1200 μmol/m²s. The measurements started at ambient light conditions and were reduced to reach zero, then followed by a gradual increase toward maximum values to allow acclimation of stomatal conductance to each condition. A-C_i curves were established to compare and define assimilation response of trees (A) to different intercellular CO₂ concentrations (C_i). Measurements were performed at constant light 1200 μmol/m²s, humidity, constant block temperature 20°C and flow 500 μmol/s, while ambient CO₂ was varied as 0, 50, 100, 350, 700 and 1000 μmol/mol. Values were recorded after assimilation response stabilized and variability became lower than 5%. Maximal assimilation (A_{max}) rates and calculated compensation points (I_{cp}) for the light

saturation and A-Ci curves were used. Water use efficiency (WUE) was calculated using the data from light curves.

Pre-dawn water potential (Ψ_{pd}) was measured on all trees between 04:00 and 04:30 every day in first week of June to estimate soil water availability in the root zone. Four leaves per tree were extracted using shears mounted on a long telescopic arm. All leaves were located on the south to southeast side of the upper third of the crown, between 20 and 25 m above ground. Ψ_{pd} for each tree was measured within a 5-min time window using a Scholander-type pressure chamber (Plant Moisture Stress, Skye, UK). All values were corrected for the hydrostatic gradient (0.01 MPa/m) based on branch height above the ground. We assumed that night-time transpiration was negligible and therefore Ψ_{pd} is representative of soil moisture availability in the rooting zone. Eco-physiological response of trees was compared with radial growth.

Growth response

Two cores were taken from every studied tree; each one was mounted and sanded to a high polish following standard preparation techniques in dendrochronology (Stokes and Smiley 1996). Cores were then digitized using ATRICS® system for image capturing and stitching (Levanič 2007) and annual radial growth measured to the nearest 0.01 mm using WinDENDRO™ software. Each tree ring series was then visually crossdated in PAST-4 using both visual on-screen comparisons and two statistical parameters t -value after Baillie and Pilcher – t_{BP} (Baillie and Pilcher 1973) and coefficient of agreement – GLK% (Eckstein and Bauch 1969). Values of t_{BP} greater than 6.0 and GLK% values greater than 65% were considered significant. The ARSTAN for Windows programme (Cook 1985; Cook and Holmes 1999) was used to remove age trend in the ring width data and build chronologies of vital and declining trees. De-trending was achieved with 67% spline. Tree-ring width indices were calculated as ratios between the actual TRW and fitted values. Index values were auto-regressively modelled and combined across all series using bi-weight robust estimation of the mean to exclude the influence of the outliers (Cook 1985; Cook et al. 1990; Cook and Holmes 1999).

Pointer years were used as a simple measure of tree response to positive or negative environmental factors, defined as years when 80% of at least 13 trees reacted with increase or decrease in growth comparing to previous year (Schweingruber et al. 1990). In case of very dry and warm years, all trees tended to reduce growth, which was visible in narrower tree-rings and vice versa. All calculations of pointer years were done on non-standardised tree-ring series.

Climate data

Despite the fact that we have local data set, we opted for a longer gridded data set from CRU (Mitchell et al. 2004). CRU TS 3.1 meteorological data set was obtained on a KNMI web page for the period 1902–2009 and grid cell N45.50–46.00, E015.00–015.50; all data sets were homogenised and error free. CRU data set was compared against local climate data set to ensure that gridded data accurately represents local climate.

Beside measured meteorological parameters Standardised Precipitation Index (SPI) (McKee et al. 1993) was calculated for the period 1902–2009 to detect dry periods, which is a measure of drought, based on the probability of precipitation for a given time period. Its key feature is the flexibility to measure drought at a different time scales; in our case we used 1, 3, 6, 12 and 24 month. From the physiological point of view, prolonged drought periods (months to years) could have important impact on tree growth, and could even cause a dieback of some tree species. Values of SPI were derived by comparing the total cumulative precipitation over a specific time interval and months with the average cumulative precipitation for that same time interval over the entire length of the record. For example: 3 months SPI for August takes into account cumulative precipitation for the last 3 months including the analysed month (June, July and August), and similarly 6 months SPI for August, takes into calculation months from March–August. Values of the SPI range from 2.00 and above (extremely wet) to –2.00 and less (extremely dry) with near normal conditions ranging from 0.99 to –0.99.

The residual chronologies were compared to meteorological data (average monthly air temperature, sum of precipitation by months and SPI for 1, 3, 6, 12 and 24 months) for the 1902–2009 period. Simple Pearson's correlation coefficient and linear models were used to test the relationship between tree growth and climate for the period 1902–2009. All statistical analysis were done in R 2.12 programme (2009).

Results

Monthly precipitation distribution and air temperature were significantly different in 2001–2010 compared with the long-term mean (1951–2000, Fig. 1). Total precipitation and mean temperature during the growing season (April–September) in 2001–2010 were 551 mm and 20.5°C, respectively, compared with the long-term mean of 598 mm and 16.2°C.

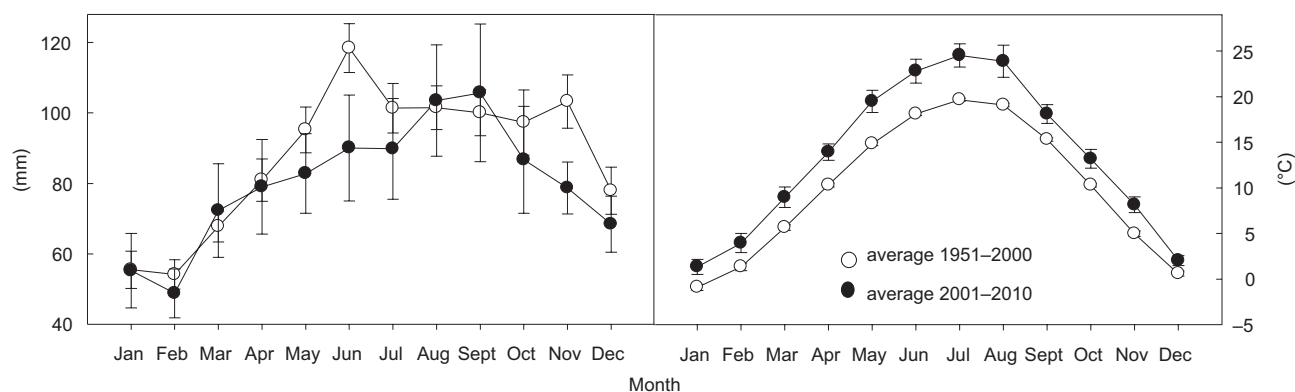


Fig. 1. Precipitation (left) and temperature (right) data of a nearby meteorological station. Monthly averages for 2001–2010 (filled symbols) and 1951–2000 (open symbols) are shown

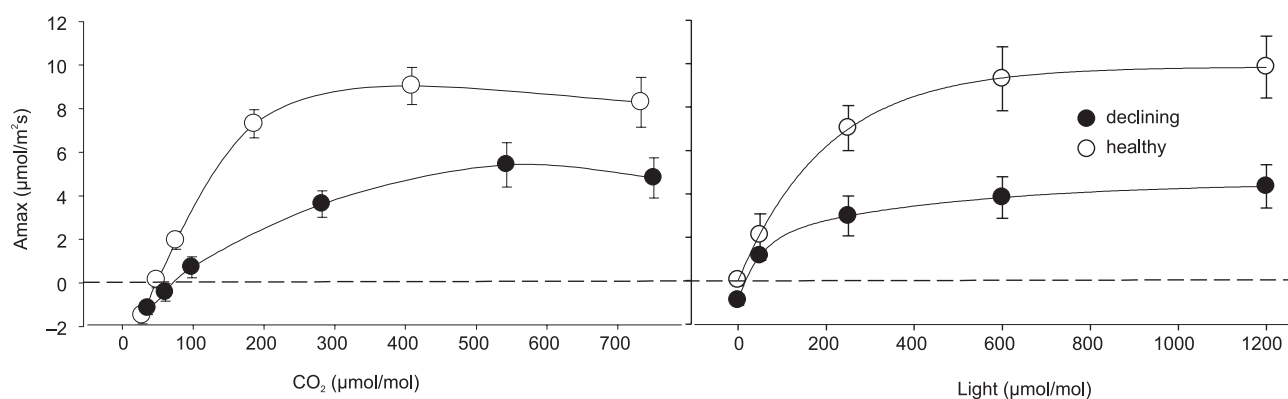


Fig. 2. Average assimilation response to different CO_2 and light intensity. Bars are standard errors

Photosynthesis and water availability

In all measured years, significant differences were observed in light response between declining and vital trees ($p \leq 0.001$) and in light compensation point, where production is balanced with consumption ($p \leq 0.001$). Comparison of response by maximal as-

similation rate (A_{max}) to different CO_2 concentration between healthy and declining trees was observed (declining: $7.8 \pm 1.2 \mu\text{mol}/\text{m}^2\text{s}$; vital: $11.2 \pm 1.4 \mu\text{mol}/\text{m}^2\text{s}$) ($p \leq 0.001$) (Fig. 2), as well as differences in CO_2 compensation points (I_c) between both groups (I_c vital: $0.58 \mu\text{mol}/\text{mol}$; I_c declining: $0.81 \mu\text{mol}/\text{mol}$) ($p \leq 0.000$) (Fig. 3).

Water use efficiency (WUE) was calculated in vital oaks 1.74 ± 0.2 , and in declining oaks 2.27 ± 0.3 [$\text{mmol CO}_2/(\text{mmol H}_2\text{O})$] ($p = 0.000$). Pre-dawn water potential (Ψ_{pd}) was also different for vital and declining trees: in vital oaks -1.18 ± 0.08 [MPa] and in declining oaks -1.52 ± 0.09 [MPa] ($p = 0.000$), insignificantly changing between observed years.

Radial growth and climate response of studied trees

Not only physiological, also growth parameters were different between studied groups, despite the fact that both analysed groups of trees have been growing on the same site with same and comparable soil conditions. The age of studied trees was comparable; declining oaks were slightly older than vital oaks, 90 and 103 year respectively. Average breast height diameter in vital group was 52.2 cm and in

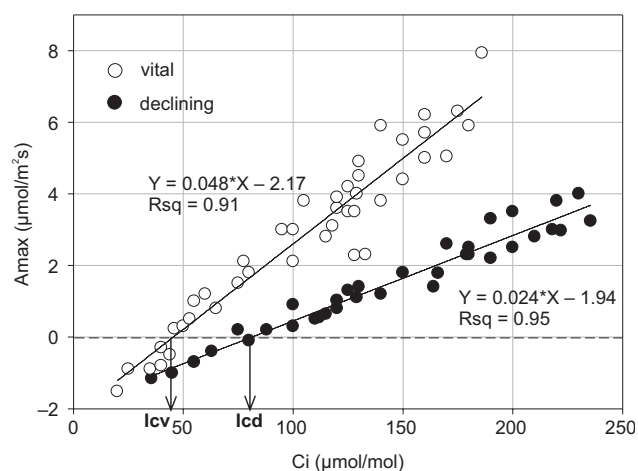


Fig. 3. Assimilation – intercellular CO_2 concentration response under standard conditions in vital and declining oaks; arrows mark the compensation points (I_{cv} – vital, I_{cd} – declining) in both groups

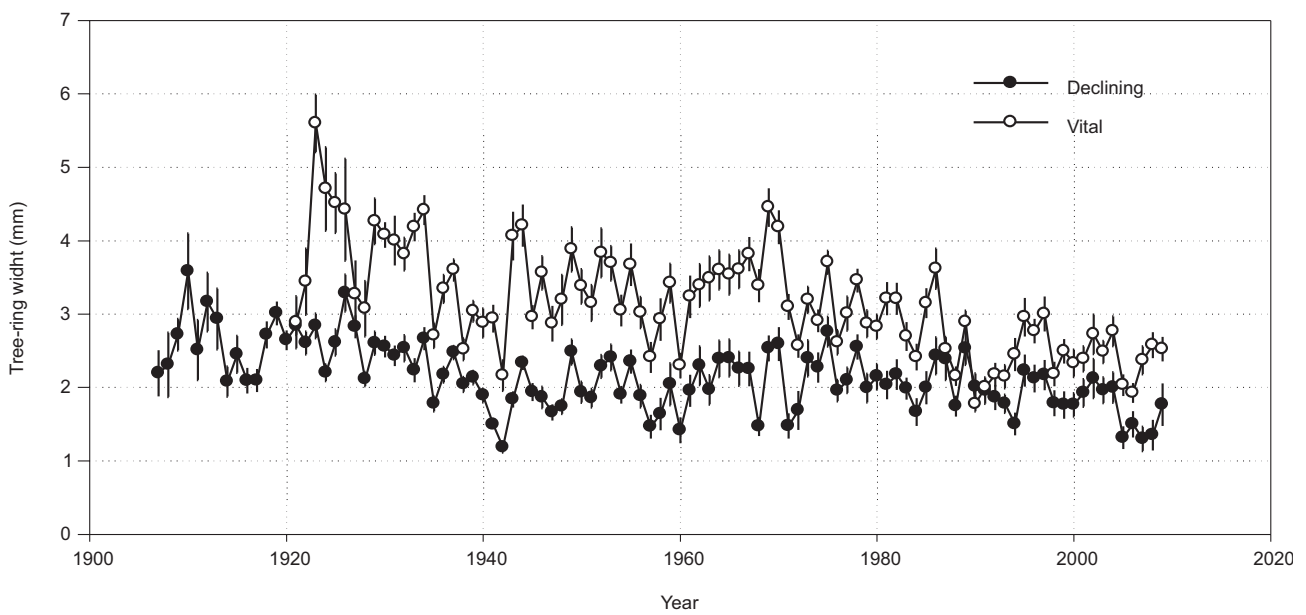


Fig. 4. Tree-ring widths for vital and declining pedunculate oaks with standard error bars

group of declining trees 35.4 cm, while average tree height (31.5 m) was the same in both groups. Since the beginning of growth vital oaks developed much wider tree-rings (3.14 ± 0.81 mm) than declining trees (2.15 ± 0.66 mm) – $p < 0.001$. Beside differences in average tree-ring width of vital and declining oaks, we also confirmed differences on a temporal scale. Vital oaks grew better throughout the entire life span, while radial increments of declining oaks were always smaller (Fig. 4).

Particularly dry and hot years, such as 1976 and 2003, had a significant negative effect on growth, while the cold and wet year 2005 had a positive influence on oaks. Growth of oaks in a floodplain forest depends mainly on the spatial and temporal distribution of precipitation during the growing season. Prolonged drought, expressed as SPI, could significantly affect radial increment and, in worst case, cause mortality. Vital oaks were more sensible to increased precipitation in early summer months – June and July,

with July precipitation being the most important for the formation of wider rings. Declining oaks indicated only response to above average July precipitation and no response to June precipitation at all. Influence of the prolonged lack of precipitation on oak growth confirmed, that declining oaks are more sensitive to lack of precipitation, they responded significantly to 3 months SPI for June, July and August. Lack of precipitation in the April – August period could significantly affect radial increment of declining trees. Vital trees, on the other hand, responded significantly only to 3-months SPI in June and July, indicating that they need sufficient supply of water in the period of most vigour growth (April – July) and less water in the second half of the summer (August) – Fig. 5.

30-year running correlation between vital and declining trees residual chronologies and June precipitation (Fig. 6) show that both groups of trees heavily rely on precipitation in first stages of their lives. Dependency then drops below significant level

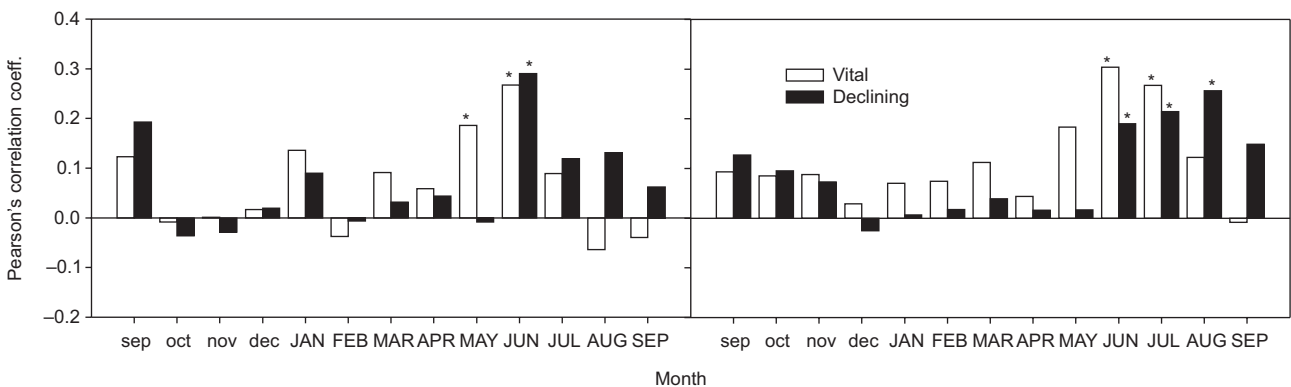


Fig. 5. Response of pedunculate oaks to the monthly sum of precipitation (left) and correlation between standardised precipitation index (SPI) and tree-ring width (right). Stars at the top of the bars represent 95% significance level of the correlation coefficients

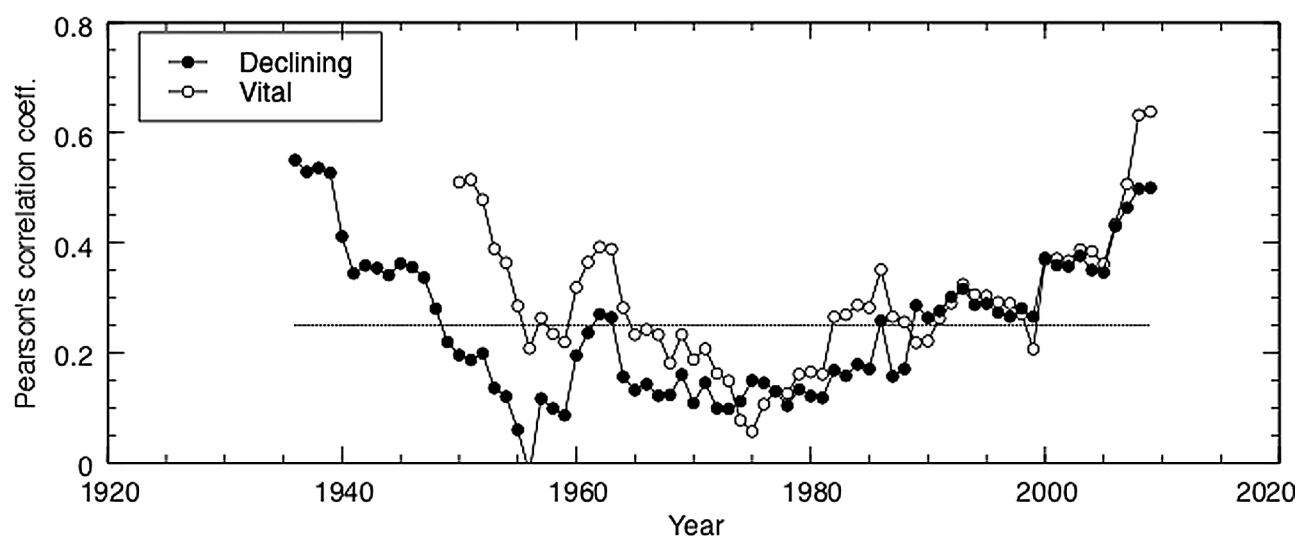


Fig. 6. 30-year running correlation between vital/declining tree residual chronology and June precipitation indicating pedunculate oak dependency on early summer precipitation. Dotted line indicates 95% significant level for running correlation

and becomes in our case again significant after 1975. Particularly high correlations during the last 10 years period coincide well with decrease in precipitation in June and July in the 1990–2010 period.

Discussion

Consequences of oak stand degradation, which caused massive oak dieback in the eighties, could be seen even today. Uneven distribution of precipitation, extreme temperatures and water pollution have disturbed the natural balance of biocenoses; they have been followed by diseases, pest attacks and general oak decline evident since the end of the 19th century (Manojlović 1926; Donaubaue 1995). Several theories have tried to explain the oak decline as the combined effect of several factors (Führer 1992; Rösel and Reuther 1995) and some have indicated possible causes in parts of Europe (Hämmerli and Stadler 1989; Hartmann et al. 1989; Näveke and Meyer 1990; Harapin and Androić 1996).

The destabilized status has been worsened by unsuitable silvicultural and technical measures in view of the changed environmental conditions (Rossel and Reuther 1995). In depth studies concerning oaks have been performed to explain disfunctions induced by water stress (Cochard et al. 1996; Triboulot et al. 1996; Tyree and Cochard 1996), links between environmental constraints and pathogens (Brasier 1996; Rubstov 1996), climate change and effects of elevated atmospheric CO₂ (Picon et al. 1996; Vivin et al. 1996), ecological and physiological analysis of decline (Thomas and Hartmann 1996), and perspective of improvement in silviculture of oaks (Gemmell et

al. 1996; Matić 1996; Wagner and Dreyer 1997; Bobinac 2000; Prpić and Anić 2000). The trend of vitality loss has been present for an extended time period, and cannot be directly linked with any single factor.

Pre-dawn water potential and water use efficiency in our study were different for vital and declining trees. Oaks growing on rich floodplain sites exhibited evident water stress, especially in group of declining trees. Lower Ψ_{pd} reduces stomatal conductance and photosynthesis, and results in embolism of pedunculate oak if water potential drops below -2.0 MPa (Tyree and Cochard 1996; Čater and Batič 2006). Changes in hydraulic conductivity occur even below -1.5 MPa (Triboulot et al. 1996; Vivin et al. 1996). Stomatal conductance decreased at Ψ_{pd} values of -1.5 MPa, to only 10% of control values (Triboulot et al. 1996; Vivin et al. 1996). Lowering of the groundwater table caused the reduction in stomatal conductivity (below 100 mmol/m²s) when Ψ_{pd} was lower than -1.2 MPa and complete closure of stomata when Ψ_{pd} was below (-1.80 – -1.95 MPa) ($F=5.95$ $p=0.024^*$) (Čater and Batič 2006).

According to WUE measurements less water was consumed in declining trees for the same amount of carbon gain for both species. Plants tend to reduce stomatal opening under water stress, so that WUE is maximized (Larcher 2003). Particularly dry and hot years, such as 1952, 1957, 1958, 1979 and 2002, had a significant negative effect on oak growth. Response function analysis showed that above average June precipitation positively influence tree-ring formation, further comparison of very narrow rings with temperature and precipitation data confirmed that – narrowest rings were associated with exceptionally dry and warm May (1958) and July (1952, 1957,

1979) and in case of 2002 with a very dry period from May–August. Interestingly year 2003, as one of the hottest and driest years in Europe, did not show in the tree-rings as particularly narrow ring. This is in accordance with our findings in oak stands in eastern Slovenian lowland. From the point of oak growth was 2002 more severe than dry 2003 and also in a different time of growing period.

The measurements of light (and CO_2) assimilation responses confirmed differences between both studied groups. Maximal assimilation rate in the vital oak group (approx. $8\text{--}10 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was below the measured response of healthy oaks ($10\text{--}15 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on other comparable sites in all studied years (Čater and Batič 2006). Assimilation response to different ambient CO_2 concentration and constant light conditions showed different response ability e.g. carboxylation efficiency in both groups. Significant difference between both compensation points according to different angle of the response curve (Fig. 2) indicated the presence of carbon starvation – limited carbohydrate availability in spite of sufficient nutrient status (Čater et al. 2008).

Declining trees formed only 1–2 rows of earlywood vessels without latewood, while vital trees continued to produce multiple (2–4) rows of earlywood vessels, normally more than 2 mm wide, as well as latewood (Levanič et al. 2011). In the ring-porous oaks, earlywood is formed using photosynthate from carbohydrates assimilated during previous year, while latewood from current year. Availability of photosynthates for stemwood growth was therefore particularly low in the declining trees. It is our belief that vital oaks are considered vital only in comparison with severely affected and almost dying oaks. Not only number of rows of vessels in earlywood, but also anatomical characteristics of vessels seem to play important role in oak mortality – large diameter vessels are prone to irreversible cavitation and, in conditions of reduced water availability play crucial role in oak mortality. Levanič et al. (2011) described that oak predisposed to die may have been hydraulically underbuilt for dry conditions, which makes them more exposed to severe hydraulic constraints and subsequent mortality.

Increased defoliation, reduced radial growth and reduced individual response indicate questionable perspective and weaker adaptation ability of adult oaks, as the defoliation variability in years becomes narrower (Čater 2015). Similar conclusions are reported for Croatian lowland oak forests by Matic (2009). Drop in groundwater table during last decade combined with weather extremes resulted in large-scale dieback of mature and senescent stands in 40% of all present pedunculate oak forests, causing changes in stand density and structure (Čavlovič et al. 2009). A number of different silvicultural ap-

proaches is discussed to adjust recent management praxis to recent structural and stand conditions in changing environment (Matić 2009).

The conditions and resulting growth patterns that oaks experience early in life may predispose them for survival or mortality when the climate and soil water conditions change to conditions which they have not previously experienced (Levanič et al. 2011). Potential physiological mechanisms may include carbon starvation – the failure to maintain metabolism and fend off pests due to limited carbohydrate availability, hydraulic failure – irreversible desiccation when embolism is not repaired (McDowell et al. 2008) or interaction between both (McDowell and Sevanto 2010). Studies of various parameters in relation to decline in oaks have only confirmed a parallel between dieback, crown diameter and the social status of trees in the stand. Trees with wider crowns and larger breast diameter were least affected (Marcu 1987; Harapin and Androić 1996), while other studies in climate-associated events have shown that both particularly high and particularly low growth can be associated with mortality (Jenkins and Pallardy 1995; Haavik et al. 2008; Wyckoff and Bowers 2010).

Although a large leaf area should be an advantage in periods of sufficient water availability, it could also predispose trees to severe water stress when water availability declines, because of higher transpirational demand (McDowell et al. 2006). Reduction in leaf area is well known drought adaptation in *Quercus* and also other tree species (Limousin et al. 2010).

Studies of sessile oak mortality (*Q. petraea*) by Thomas and Hartmann (1996) and Thomas et al. (2002) have shown lower root biomass in dying trees. Differences could cause higher nutrient availability and consequently higher photosynthetic capacity or better water availability in early stages of life. In periods of drought, lower root mass proportion would cause faster hydraulic failure and carbon starvation, since present water availability would not meet the demands of the transpiration.

Bobinac and Andrašev (2009) connect devitalisation process on comparable sites in northern Serbia directly with stand structure and silvicultural treatments. Intensive tending (removal of strongest competitors from the future-trees) applied in the 42 year resulted on average with 37% higher radial increment at the age of 52 compared to the plot with sanitary cut where only drying stems were removed. In parallel study, the drought adaptation in adult oak leaves was measured during two growing seasons (2003 and 2004) in the same forest district site in Slovenia. Managed forest with lower stand density indicated highest osmotic adaptation, e.g. most negative values in spite of its age, compared to managed forest plot ($\text{df}_{2,8}$; $F=4.52$, $p < 0.05$) and old growth forest ($\text{df}_{2,8}$; $F=5.17$, $p < 0.05^*$), while values of pre-

dawn water potential in all three plots remained similar (Čater 2011). Values became more negative from June to August indicating ability of oaks to adapt with increasing water deficit on all sites. Despite the apparent homeostatic ability of oaks to compensate drop of groundwater table and water stress, such adaptation did not contribute to long-term improvement of adult trees.

Conclusions

Lowland oak forests are threatened mainly by the conversion of forests into agricultural land where relatively small remaining forest patches are affected by the rapidly changing environmental factors. It is our belief that dieback and loss of individual response in gradually induced by reduced water availability – the altered groundwater table since the late 1980's, accompanied by the precipitation redistribution which adult oak trees are no longer able to compensate and adapt. In spite of well-known regeneration ability, oaks cannot successfully replace increasing loss of assimilation area, so physiologically weakened trees become even weaker. Radial increment in oaks is small; responses to climate are evident only in the group of vital trees, while declining trees respond with a further growth decrease and finally die, as confirmed by our study. In the future oak trees may exhibit greater rates of mortality, particularly on sites of prior fast growth, if predictions of increased drought severity and frequency are accurate.

Acknowledgement

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