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Osmotic adaptation of *Quercus robur* L. under water stress in stands with different tree density – relation with groundwater table

Received: 11 January 2011; Accepted 26 April 2011

Abstract: Solute accumulation in plant leaves during drought through accumulation of organic compounds is known to compensate turgor loss and promote higher stomatal conductance at lower water potentials. Recent studies have involved experiments on saplings and younger stands, while evidence of osmotic adjustment in adult pedunculate oak under natural stand conditions on different sites is scarce.

Pressure volume curves technique was used to define differences in osmotic potential – water stress adaptation – of 120 year old pedunculate oak trees in two managed forest complexes and in virgin forest remnant. Tree response between the managed stand after thinning and the stand without any silvicultural measures within same forest complex was also compared during summer months in two consecutive (dry and favourable) years with groundwater table.

Significant differences were observed in adaptation between forest complexes and during dry (2003) and favourable (2004) years. Osmotic component of thinned forest was the highest, showing most negative values of stress adjustment. Measured values on all plots responded well to drop in groundwater table, especially in pronounced drought conditions. Such response may be in relation with lower stand density and increased individual space for growth in thinned stand. Adult oaks did not lose their ability to water stress adaptation, in spite of their age and progressively decreasing health conditions.

Additional key words: osmotic water potential, groundwater table, PV curves, pedunculate oak, stress adaptation, floodplain forests

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Introduction

Water availability is, together with radiation, a limiting factor in the occurrence, abundance and growth of trees on certain sites (Kramer 1969). Under low water supplies species with a larger tolerance to water stress (early successional) are able to maintain higher gas exchange rates than those less tolerant (Ni and Pallardy 1991). The capacity to absorb water from the soil and transfer it to the atmosphere is a decisive factor in the response of species to water stress (Pallardy 1989).

Numerous studies involving a wide range of plant growth forms and habitats have demonstrated osmotic adjustment in plant tissue during drought (Hanson and Hitz 1982, Jefferies 1981, Morgan 1984). Solute accumulation in leaves and roots of pedunculate oak (*Quercus robur* L.) aided in maintenance of turgor and high leaf conductance during water stress (Osonubi and Davies 1978). Significant change in osmotic potential (increase of soluble compounds concentration) during drought were evident in *Quercus alba* and *Quercus rubra* (Parker et. al. 1982), which in turn promoted higher stomatal conductance

at lower water potentials. The ability of plants to tolerate water deficits has been frequently attributed also to their capacity for osmotic adjustment through accumulation of organic compounds such as amino-acids or soluble carbohydrates (Turner and Jones, 1980; Morgan, 1984). It is thought that the production of osmotic solutes (such as sugars derived from the degradation of starch) creates a high turgor in xylem parenchyma cells, which then causes some squeezing out of water from the tissue protoplasts into vessel lumina (Canny 1998). Others have speculated that water would be driven into cavitating vessels by capillary forces (Holbrook and Zwienicki 1999, Zwienicki and Holbrook 2000). This, in turn, would increase the volume of droplets sitting at the vessel walls at atmospheric pressure or nearly so. A positive pressure would be created in the liquid phase that would compress the air and eventually remove it from the vessel.

The characteristic relationship between the water potential of plant organs and the state of hydration can be illustrated by pressure-volume (P/V) curves (Tyree and Hammel 1972) in which the decrease in cellular pressure with progressive loss of water is related to the decrease in volume. The water potential is substituted for pressure, and the relative water content (RWC) for volume (Larcher 1995). P/V curves are generated by measuring the weight and corresponding water potential of studied (drying) plant material (e.g. leaves, shoots) and plotting the relationship of the water potential to inverse of the relative water content or inverse of the water expressed from the plant material (Abrams 1988). The linear portion of the curve, established after the tissue turgor loss point, is used to estimate the osmotic potential at full and zero turgor, by extrapolating the line to the y-axis (Abrams 1988) (Fig. 1).

Lowland oak forests in Slovenia are submitted to temperate climate, but they encounter periods of severe drought which are known to be involved in forest decline processes (Čater 2003) as well as limiting forest primary productivity and tree growth (Aussenac 1978, Becker and Levy 1982). Except for floodplain characteristics, pedunculate oak forests represent the most artificially changed forests in Slovenia as well as in lowlands of other European countries. Originally, their natural range coincided with that of the nowadays most intensely managed agricultural land (Čater and Batič 2006).

Larger complexes of pedunculate oak are now restricted to small areas and found only in moist sites less suited for agriculture. Significant correlation has been confirmed between groundwater table and pre-dawn water potential (Čater et al. 1999), groundwater, precipitation and defoliation of pedunculate oaks (Čater 2003) and also between groundwater table, water potential and stomatal conductance in dif-

ferent light categories of planted and naturally regenerated saplings of pedunculate oak on two different sites (Čater and Batič 2006). Question about adult oak ability to osmotically compensate water stress has not been confirmed in studied forest complexes, since their condition is not improving according to their radial growth and status of crown transparency (Levanič and Čater 2007).

In the following study the change of full turgor osmotic component (derived from pressure-volume curves) for pedunculate oak during two growing seasons on two different lowland sites is presented. Objectives of study were to define differences in stress adaptation between two oak managed forest complexes and virgin forest remnant (1); to compare species response between adult stands after stronger thinning and without any silvicultural measures within same forest complex (2) and to confirm the connection between stress adaptation and groundwater table on studied sites (3).

Material and Methods

Experiment was carried out in two forest complexes – the first located in the northeast of the country and severely damaged by the drought stress (Murska šuma) and on a reference site in the south-east of Slovenia (Krakovo forest), better supplied with water and showing less damaged status of adult oak trees. On every location five adult and dominant trees were selected and leaves from the same height, upper crown position and orientation were sampled and analyzed. In Murska šuma two locations with low and high groundwater table were included into the study (Čater and Batič 2006) (M1 and M2 respectively) and compared with less stressed locations in Krakovo forest: i) managed stand (K1), ii) managed stand with reduced stand density (K2) and iii) virgin forest of pedunculate oak and hornbeam (K3) with same groundwater conditions (Table 1). On plot K2 35% of living stock (close to 500 m³/ha) was removed in 2002 as the final cut and approximately 40–45 trees/ha remained. Sets of pressure volume measurements (PV) were performed during two weeks in June, July and August 2003 and 2004. Paralely, measurements of pre-dawn water potential with pressure chamber (SKYE) were measured at the same sites with known groundwater table status (Čater and Batič 2006).

In 2003 severe drought with above average air temperatures and lower amount of precipitation was evident in lowlands, while no significant deviations from 30 year average values were confirmed in 2004 (Table 2). Differences in precipitation arrangement were evident in Lendava; in 2003 lack of precipitation was present from March and lasted until August. Cumulative amount of precipitation in vegetation period

Table 1. Plot characteristics (for the description see text)

Plot	Soil type	Stand density dbh>10 cm (n/ha)	Living stock (m ³ /ha)	Stand age (years)	Lat (°)	Long (°)
M1	Eutric gleysols	155	430	138	46°30'27.9"	16°31'05.9"
M2	Eutric fluvisol	150	420	145	46°29'18.3"	16°32'41.7"
K1	Eutric gleysols	160	450	135	45°53'00.9"	15°25'03.0"
K2	Eutric gleysols	45	175	140	45°53'00.5"	15°25'25.1"
K3	Eutric gleysols	120	750	220	45°52'25.1"	15°42'25.3"

Table 2. Monthly indexes for the precipitation and average air temperatures compared to 15 year average values (1991–2006) for Lendava (161 m a.s.l.) near Murska šuma (M1, M2) and Novo mesto (188 m a.s.l.) near Krakovo forest (K1, K2, K3)

Precipitation index	Year	March	April	May	June	July	August
Lendava	2003	0.05	0.19	0.34	0.64	0.58	0.26
	2004	2.34	1.82	0.83	1.45	0.44	1.77
Novo mesto	2003	0.10	0.67	0.32	0.61	0.45	0.35
	2004	1.77	1.15	0.95	0.85	0.97	0.90
Temperature index	Year	March	April	May	June	July	August
Lendava	2003	1.04	0.94	1.17	1.21	1.06	1.18
	2004	0.76	1.01	0.87	0.94	0.97	0.99
Novo mesto	2003	1.03	0.94	1.16	1.21	1.06	1.18
	2004	0.70	1.01	0.88	0.95	0.97	0.99

(March–August) reached only 35% of 15 year average values, while in Novo mesto amount was higher (42%). Rain deficite coincided with high temperatures (10% higher in both Lendava and Novo mesto). In 2004 amount of precipitation was higher with peaks in April, June and August for Lendava and close to averages for Novo mesto – the temperatures in 2004 were lower than average values.

P-V curves were determined using a Scholander pressure chamber (Scholander et al. 1965) and following the free-transpiration as described by Talbot et al. (1975), Hinckley et al. (1980), Turner (1980) and Dreyer et al. (1990). Branches were collected in the late afternoon, recut under water in the lab to resaturate in distilled water overnight. At periodic intervals, the weight and water potential of each branch were measured. The weight and water potential were measured at constant time intervals until values close to $-2,5$ MPa were reached.

Relative water content of sampled leaves (RWC) was determined by the equation (1) presented by Larcher (1995):

$$RWC(\%) = \frac{m_{\text{moment}} - m_{\text{dry}}}{m_{\text{saturated}} - m_{\text{dry}}} \times 100\%, \text{ where} \quad (1)$$

m_{moment} ... momentary weight of measured leaf (g);
 m_{dry} ... dry leaf mass (24 hours at 105°C) (g),
 and
 $m_{\text{saturated}}$... with water saturated leaf mass (g).

Osmotic component (Ψ_{π}) was determined by the extrapolation of linear part of the curve, crossing the y-axis as presented in Figure 1. Values of osmotic potential at full tissue saturation ($\Psi_{\pi 100}$) (Fig. 1, point 1) were estimated from plots of $1/RWC$ vs PWP using a weighed linear regression technique (Bahari et al. 1985) and compared between studied parameters between different pedunculate oak stands. Meteo data (temperature, precipitation) was obtained from closest hydrometeorological stations (Lendava and Novo mesto, ARRS), while groundwater table was mea-

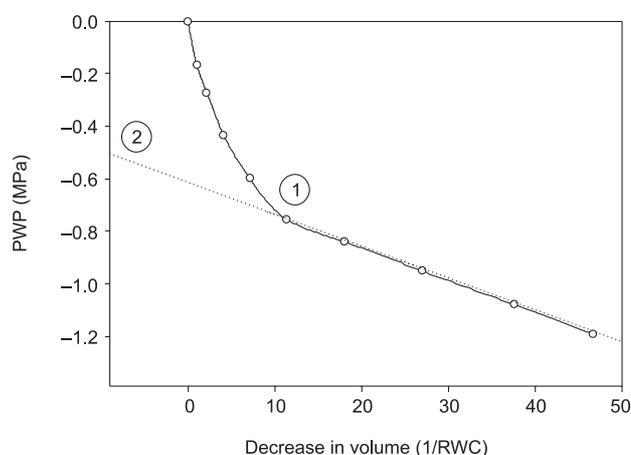


Fig. 1. Schematic review of ideal PV curve (after Abrams 1988): beyond the zero turgor point (1) the measured water potential corresponds to the osmotic potential. As the linear part of the curve is extended to the ordinate (2), the intersection yields the osmotic potential at turgidity

sured from pre-installed (1998) piezometers on plots and corresponded exactly to the time when leaves were sampled for the osmotic potential measurements. Statistical differences between groups were considered significant at level $p=0.05$ (*), $p=0.01$ (**) and $p=0.001$ (***); all analysis (AVAR, t-tests) were performed with programme R (<http://www.r-project.org/>).

Results

Significant differences were confirmed in osmotic potential component for plots in Murska suma in 2003 between plots (M1, M2) ($df_{2,8}$ $F=8,73$ ***) in July and August and also in Krakovo forest between managed forest (K1) (more negative values,) and old growth-forest (K3) (less negative values, $df_{2,8}$ $F=5,01$ **). Values in Murska šuma forest complex were significantly lower from those in Krakovo forest as the stress was more severe in northeast of the country (Table 3).

In 2004 relation between plots remained unchanged, but the absolute values were smaller, which could be connected with better water supply and smaller water deficit in both forest complexes. Differences between plots in Murska šuma were insignificant, but the managed forest with lower stand density again indicated highest adaptation, e.g. most negative osmotic component value on plot K2, compared to other managed forest plot (K1) ($df_{2,8}$ $F=4,52$ *) and old growth forest (K3) ($df_{2,8}$ $F=5,17$ *) (Table 4). Values of pre-dawn water potential in all three plots were similar (data not shown).

It was interesting to compare reaction of forests adaptation after thinning (K2) and managed forest (K1) in Krakovo forest: values of osmotic potential before thinning were the same as in the managed forest, while after cutting of approximately 35% of living stock (2002) the response of remaining trees indicated well adapted mechanism to address drought stress in spite of their age. In the other managed forest (K1) adult trees of the same age did not exhibit such physiological response, which was similar to the response observed in the old growth forest.

Comparison of osmotic adaptation in leaves with groundwater table showed similar and highly corre-

lated pattern of adaptation in Murska suma (M) which also corresponded well with groundwater table in both years. Thinned stand in Krakovo forest (K2) exhibited much lower values according to the similar groundwater status conditions on other plots (K1 and K3, respectively) (Fig. 2).

Discussion

Ecological studies conducted in oak stands have shown differences between different oak species (Epron and Dreyer 1996). A variety of mechanisms may be responsible for these differences such as better soil colonization by roots, more efficient control of water loss during stress periods, and/or a better ability to tolerate leaf water deficits. It is generally accepted that the best criterion for desiccation tolerance is the ability to maintain a high turgor when transpiration or soil water conditions impose a low leaf water potential (Turner, 1980). Relationships between mean parameters of P-V curves show clear differences between species in this respect. The degree of desiccation tolerance is highest in mediterranean *Q. ilex*, followed by *Q. pubescens* and *Q. petraea* and finally by *Q. robur* (Dreyer et al. 1990). Indicators for water supply in trees also differ significantly between species and especially in oaks. According to Methy et al. 1996) changes in hydraulic conductivity in *Q. ilex* and *Q. pubescens* occur below -4.0 MPa, whereas according to Tyree and Cochard (1996) and Tognetti et al. (1996) below -6.0 MPa. Changes in *Q. rubra* appear below -2.3 MPa (Tyree and Cochard 1996). Pedunculate oak is more sensitive when compared to sessile oak (Dickson and Tomlinson 1996) as regards cavitation and embolism of vessels (Cochard et al. 1996, Tyree and Cochard 1996, Timbal and Aussenac 1996). Changes in hydraulic conductivity occur below -1.5 MPa (Tribolout et al. 1996, Vivin et al. 1996).

Since many researchers report that osmotic potential at turgor loss point follows the similar pattern of variation to the one at full turgor (Aranda et al. 1995, Corcuera et al. 2002) we were focused on values at full turgor which confirmed known pattern for osmotic potential to decrease (and become more negative) as the soil drought increases. There were no precipitation in both forest complexes in 2003 during

Table 3. Full turgor osmotic component ($\Psi_{\pi 100}$) in adult tree leaves (MPa) on research plots in 2003: average values for plots with standard errors of means are presented.

Plot	June	July	August
M1	-1.36 ± 0.03	-1.42 ± 0.06	-1.48 ± 0.08
M2	-1.33 ± 0.08	-1.31 ± 0.04	-1.33 ± 0.09
K1	-1.26 ± 0.05	-1.25 ± 0.08	-1.27 ± 0.07
K2	-1.39 ± 0.09	-1.43 ± 0.08	-1.47 ± 0.09
K3	-1.22 ± 0.07	-1.28 ± 0.05	-1.20 ± 0.06

Table 4. Full turgor osmotic component ($\Psi_{\pi 100}$) in adult tree leaves (MPa) on research plots in 2004: average values for plots with standard errors of means are presented.

Plot	June	July	August
M1	-1.33 ± 0.07	-1.33 ± 0.06	-1.36 ± 0.05
M2	-1.25 ± 0.06	-1.27 ± 0.09	-1.23 ± 0.09
K1	-1.23 ± 0.06	-1.25 ± 0.07	-1.25 ± 0.08
K2	-1.33 ± 0.08	-1.34 ± 0.07	-1.36 ± 0.09
K3	-1.21 ± 0.05	-1.23 ± 0.06	-1.24 ± 0.05

our measurements, while in June and August 2004 the amount of rainfall reached above average values for the Murska šuma complex (Table 2) that lead to non significant differences between osmotic adjustment between plot with low and high groundwater table. In Krakovo forest complex stand density affected water stress in adult oaks; most evident adaptation was seen in thinned stand (where regeneration cutting began), smaller in unthinned managed forest and smallest in old growth forest, showing insignificantly different response to the one observed in the thinned managed forest. In all cases measured values became more negative from June to August indicating ability of oaks to adapt with increasing water deficit.

Osmotic adjustment of adult oaks responded well with changes in groundwater table, where response

on both plots in Murska šuma followed similar pattern, especially when drought in 2003 was pronounced, while differences in Krakovo forest were seen in smaller scale. Pattern of adaptation in unthinned managed forest plot (K1) and plot in old growth forest (K3) was significantly different from thinned forest (K2), showing much better adaptation to the same groundwater condition on all plots within studied forest complex. Such response may be connected with better physiological response of adult trees because of reduced competition and wider individual growing space in stands with lower tree density and possible pronounced effects on the carbohydrate content of leaves as reported by Epron and Dreyer (1996). Pre-dawn water potential measures between plots in Krakovo forest did not differ significantly, exposure of trees to water stress was similar.

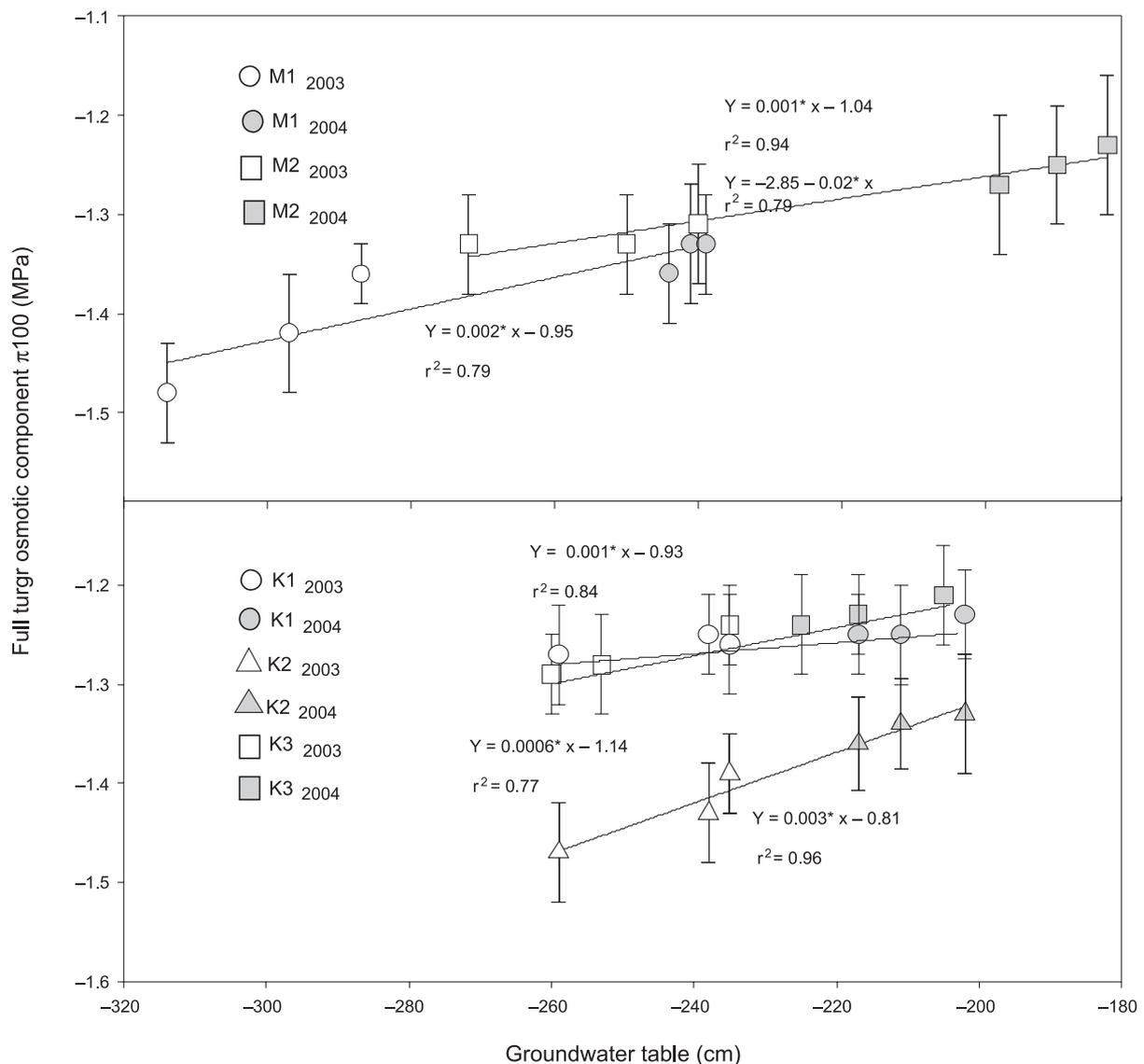


Fig. 2. Osmotic component vs. groundwater table in 2003 and 2004 for two forest complexes: Murska šuma (M1 – plot with high groundwater table, M2 – plot with low groundwater table; both managed forests) and Krakovo forest (K1 – managed forests plot, K2 – managed forest plot with reduced stand density and K3 – old growth forest plot), with same groundwater table on all plots

Results responded well with critical groundwater table values defined for the survival of young oaks according to the stomata closure and pre dawn leaf water potential (Čater and Batič 2006), where young oaks in North eastern part (Murska šuma) exhibited stomata closure at lower groundwater table values (critical value at -270 cm) compared to oaks from Krakovo forest (-240 cm, respectively), showing different adaptation to water stress for growing in better conditions of water supply.

Analysis of radial growth and its relation to climate confirmed reduced radial growth, critically high crown defoliation and increasing mortality on permanent research plots with pedunculate oaks with increasing number of extreme weather events; tree rings become narrow and trees consequently loose their ability to adapt to rapid environmental changes (Levanič and Čater 2007). After extremely hot or dry years (such as 2003), the average crown defoliation according to forest survey inventory (Anonymous 1994) increased and has not improved since 2000. Not only the increased defoliation and reduced radial growth, but also reduced individual response indicate questionable perspective and weaker adaptation ability of adult oaks on studied plots, as the dispersion in years becomes more and more narrow (Fig. 3). Similar conclusions are reported for Croatian lowland oak forests by Matić (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 (Čavlović et al. 2006). A number of different silvicultural approaches is discussed to adjust recent management praxis to recent structural and stand conditions in changing environment (Matić 2006).

Studied parameters could explain the pattern of species response with regard to rainfall shortage, and lack of water availability (lower groundwater table) which is a frequent situation in the area during the summer months.

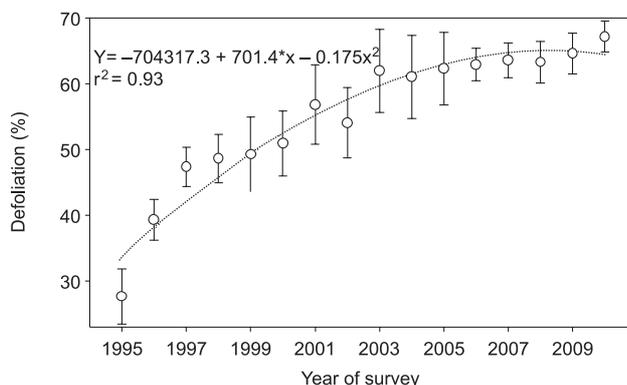


Fig. 3. Defoliation of pedunculate oak crowns on permanent research plots

In spite of their well-known regeneration ability, oaks hardly replace increasing loss in assimilation area, so physiologically weakened trees become even weaker. As the condition of adult oaks in Slovenian lowlands is not improving, it was against our common expectation to evidence such physiological response on site conditions with reduced water availability in stands that are losing their response ability to environmental changes (Čater 2003). Evidently oaks don't lose all adaptation ability with age, but are still able to withstand drought conditions during shorter time intervals. Results should be however, interpreted with caution, since adaptation may be possible only until the irreversible threshold for water stress is reached.

Acknowledgement

Presented research was financially supported by the Slovenian Research Agency grant L4-9653 Influence of climate change on growth response of Pedunculate oak (*Quercus robur* L.) and European larch (*Larix decidua* L.) and V4-0348 Influence of climate change on growth and tree response on Slovenias extreme sites supported by the Slovenian Research Agency, Ministry of Food, Agriculture and Forestry and Slovenian Research Agency and Programme Research Group. Special thanks to doc. Tom Levanič for constructive suggestions about data presentation and two anonymous reviewers for their comments for improving the quality of text.

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