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Osmotic component of water potential and stress adaptation of adult Pedunculate oaks (*Quercus robur* L.) in stands with different tree density

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Abstract

Pressure volume curves were applied to define differences in stress adaptation between two managed forest complexes and virgin forest remnant; in Murska šuma, Krakovo forest and Krakovo old growth forest. Species response between adult stands after stronger thinning and comparable stand without any silvicultural measures within same forest complex was compared in two consecutive years, 2003 and 2004.

Significant differences in osmotic potential (full turgor) component for plots in Murska šuma in 2003 as well as in Krakovo forest between managed forest and old growth-forest were confirmed. In all cases, values became more negative, indicating slight capability of oaks to adapt with increasing drought stress. Reaction/stress adaptation of forests after thinning indicated well adapted mechanism to address drought stress in spite of the age. We may connect such improved drought response with increased individual space for growth and lower stand density.

Key words: osmotic water potential, P/V curves, pedunculate oak, *Quercus robur* L., drought stress adaptation, floodplain forests

Osmotska komponenta vodnega potenciala in prilagoditev odraslih dobovih sestojev (Quercus robur *L.*) *na sušni stres z različno sestojno gostoto*

Izvleček

Za primerjavo in opredelitev razlik stresnega prilagajanja na sušo odraslih dobovih sestojev smo uporabili P/V-krivulje; primerjali smo odzive gospodarskega gozda v Murski šumi, v Krakovskem gozdu in pragozdnega rezervata Krakovo kot tudi gospodarska sestoja z različno drevesno gostoto (redčen sestoj, neredčen) v poletnih mesecih 2003 in 2004.

Potrdili smo značilne razlike v osmotski komponenti vodnega potenciala pri polnem turgorju med ploskvama Murske šume in Krakovskega gozda. Na vseh ploskvah je bilo opaziti povečevanje osmotske komponente z naraščanjem sušnega stresa. Sestoj po redčenju / uvajanju v obnovo je pokazal dobro oblikovan mehanizem in prilagajanje kljub starosti, najverjetneje zaradi sproščene konkurence in povečanega rastnega prostora.

Ključne besede: *osmotska komponenta, vodni potencial, P/V krivulje, dob, Quercus robur* L., *sušni stres, prilagoditve, nižinski gozdovi*

1 Introduction

1 Uvod

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 greater 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 decreases in osmotic potential (increase of soluble compounds concentration)

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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 cavitated 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 (ABRAMS 1988). The linear portion of the curve, established after the tissue turgor loss point could be used to estimate the osmotic potential at full and zero turgor, by extrapolating the line to the y-axis (ABRAMS 1988) (Figure 1).

Lowland oak forests are submitted to temperate climate, but they encounter periods of severe drought, which are known to be involved in decline processes and to limit forest primary productivity and tree growth (AUSSENAC 1978, BECKER and LEVY 1982). Except for floodplain characteristics, pedunculate oak forests constitute the most 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 nutrient status (ČATER *et al*. 1999), groundwater, precipitation and defoliation of pedunculate oaks (ČATER 2003), as well as between groundwater table, water potential and stomatal conductance in different light categories of planted and naturally regenerated saplings of pedunculate oak (ČATER and BATIČ 2006) on two different sites. The question about oak ability to osmotically compensate water stress has not been confirmed in the studied forest complexes. In the present study, the change of some water potential parameters derived from pressure-volume curves during two growing seasons for pedunculate oak on two different lowland sites is presented. The studied parameters could explain the pattern of species response with regard to rainfall shortage, which is a frequent situation in the area during the summer months.

Objectives of the study were:

1. to define differences in stress adaptation between two oak managed forest complexes and virgin forest remnant;
2. to compare species response between adult stands after stronger thinning and comparable stand without any silvicultural measures within same forest complex.

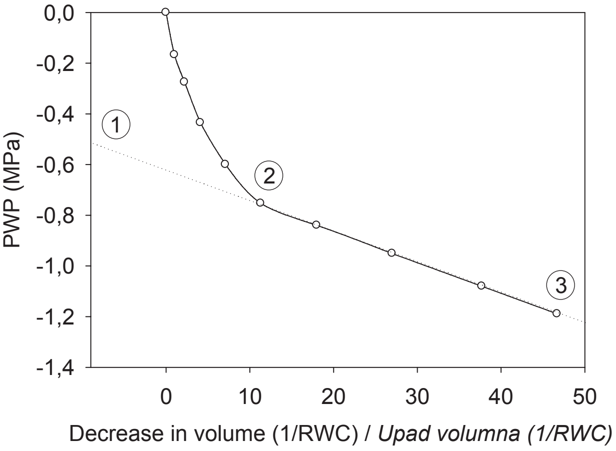

Figure1: Schematic review of ideal P/V curve (after Larcher 1995)

Slika 1: Shematski prikaz poteka idealne P/V-krivulje (povzeto po Larcher 1995)

2 Material and methods

2 Materiali in metode

Experiment was carried out in two forest complexes - the first located in the northeast of the country and severely damaged by drought stress (Murska šuma), and on a reference site in the southeast of Slovenia (Krakovski gozd), 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, 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 Krakovski gozd: i) managed stand (K1), ii) managed stand with reduced stand density (K2) and iii) virgin forest of pedunculate oak and hornbeam (K3) (table 1). On plot K2, 35% of living stock (close to 500 m^3/ha) was removed in 2002 as the final cut and approximately 40-45 trees/ha remained. Sets of pressure volume measurements (P/V) were performed during two weeks in June, July and August 2003 and 2004. Parallely, measurements of pre-dawn water potential with pressure chamber (SKYE) were carried out 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 prevailed from March until August. Cumulative amount of precipitation in vegetation period (March-August) reached only 35% of 15-year average values, while in Novo mesto the amount was slightly higher (42%). Rain deficit coincided with high temperatures (10% higher in both Lendava and Novo mesto). In 2004, the amount of precipitation was higher with peaks in April, June and August for Lendava and close to averages for Novo mesto, where the temperatures in 2004 were even 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 potentials of each branch were measured. The weight and water potentials 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):

$$RWC(\%) = \frac{m_{moment} - m_{dry}}{m_{saturated} - m_{dry}} X100\% \quad \text{, where} \qquad (1)$$

m_{moment}…momentary weight of measured leaf (g);

m_{dry}… dry leaf mass (24 hours at 1050C) (g), and

$m_{saturated}$… 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.

Table 1: Plot characteristics

Preglednica 1: Lastnosti raziskovalnih ploskev

Plot / *Ploskev*	Soil type / *Talni tip*	Stand density (n/ha), dbh>10cm / *Gostota sestoja (n/ha), dbh>10cm*	Living stock (m^3/ha) / *Lesna zaloga (m^3/ha)*
M1	Eutric gleysols	155	430
M2	Eutric fluvisol	150	420
K1	Eutric gleysols	160	450
K2	Eutric gleysols	45	175
K3	Eutric gleysols	120	750

Table 2: Monthly indexes for the precipitation and average air temperatures compared to 15-year average values (1991-2006) for Lendava (161m a.s.l.) and Novo mesto (188m a.s.l.)

Preglednica 2: Mesečni indeksi padavin in zračnih temperatur glede na 15-letno povprečje (1991-2006) za Lendavo (161m n.m.) in Novo mesto (188m n. m.)

Precipitation index / *Indeks padavin*		March / *marec*	April / *april*	May / *maj*	June / *junij*	July / *julij*	August / *avgust*
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 / *Indeks temperatur*		**March / *marec***	**April / *april***	**May / *maj***	**June / *junij***	**July / *julij***	**August / *avgust***
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

Values of osmotic potential at full tissue saturation($\Psi_{\pi100}$) (Figure 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 were obtained from closest hydrometeorological stations (Lendava and Novo mesto, ARRS). Statistical differences between groups were considered significant at level $p \leq 0.05$; all analyses (AVAR, t-tests) were performed with programme R.

3 Results

3 Rezultati

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

In 2004, relation between plots remained, 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) and old growth forest. Values of pre-dawn water potential in all three plots were similar, indicating no water stress (data not shown).

It was interesting to compare the reaction of forests adaptation after thinning (K2) and managed forest (K1) in Krakovo forest: osmotic adaptation before thinning was same as in the managed forest, while after cutting of approx. 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.

4 Discussion

4 Razprava

Since many researchers report that osmotic potential at turgor loss point follows a similar pattern of variation to the one at full turgor (ARANDA *et al*. 1995, CORCUERA *et al*. 2002), we focused on the values at full turgor and confirmed the known pattern for osmotic potential to decrease (and become more negative) as the soil drought increases. Stand density affected water stress in adult oaks;

Table 3: Full turgor osmotic component ($\Psi_{\pi100}$) in adult tree leaves (MPa) on research plots, ***2003: average values for plots with standard errors of the means are presented***

Preglednica 3: Komponenta osmotskega potenciala pri polnem turgorju ($\Psi_{\pi100}$) v listju odraslih dobov (MPa) na raziskovalnih ploskvah za leto 2003: povprečne vrednosti z odklonom zaupanja

Plot / *Ploskev*	June / *junij*	July / *julij*	August / *avgust*
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 ($\Psi_{\pi100}$) in adult tree leaves (MPa) on research plots, ***2004***

Preglednica 4: Komponenta osmotskega potenciala pri polnem turgorju ($\Psi_{\pi100}$) v listju odraslih dobov (MPa) na raziskovalnih ploskvah za leto 2004

Plot / *Ploskev*	June / *junij*	July / *julij*	August / *avgust*
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

most evident adaptation was seen in thinned stand (where regeneration cutting began), smaller in unthinned managed forest, and smallest in old growth forest. In all cases, the measured values became more negative from June to August, indicating slight capability of oaks to adapt with increasing drought stress. 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* in and finally by *Q. robur* (DREYER *et al*. 1990).

Indicators for water supply in trees differ significantly between species and especially in oaks. In submediterranean species (*Q. ilex, Q. pubescens*), changes occur in hydraulic conductivity below -4.0 MPa (METHY *et al*. 1996) and below -6 MPa (TYREE and COCHARD 1996, TOGNETTI *et al*. 1996), in *Q. pubescens* below -2.0 MPa (EPRON and DREYER 1996, BREDA *et al*. 1992) and in *Q. rubra* 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 even below -1.5 MPa (TRIBOLOUT *et al*. 1996, VIVIN *et al*. 1996).

The results 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.

Evidently oaks do not lose their adaptation ability with age, which was confirmed by our study. However, results should be interpreted with caution, since adaptation may be possible only until the irreversible threshold for water stress is reached.

5 Povzetek

Zmožnost rastlin na toleranco vodnega stresa pogosto povezujemo z njihovo možnostjo osmotskega prilagajana. Za določanje osmotske komponente vodnega potenciala se uporablja volumske krivulje (P/V krivulje), ki opisujejo odnos med skupnim vodnim potencialom in relativno vsebnostjo vode v živih rastlinskih tkivih. Sposobnosti osmotske kompenzacije vodnega stresa v nižinskih dobravah, kjer smo do sedaj potrdili značilno povezavo med stanjem hranil in podtalnico (ČATER s sod. 1999), podtalnico, padavinami in stanjem osutosti (ČATER 2003) ter podtalnico, zapiranjem listnih rež in svetlobnimi razmerami naravnega in vnešenega dobovega mladja (ČATER in BATIČ 2006) do sedaj nismo potrdili.

V članku primerjamo osmotsko prilagoditev na stres v dveh gozdnih kompleksih in pragozdu ter isti odziv primerljivih odraslih sestojev po redčenju s sestojem, kjer redčenja nismo izvedli znotraj istega gozdnega kompleksa v dveh nižinskih dobravah - Murski šumi na severovzhodu Slovenije, z večjo izpostavljenostjo vodnemu stresu in primerljivim Krakovskim gozdom na jugovzodu, ki je bolje preskrbljen z vodo. Na vsaki ploskvi smo izbrali pet odraslih, dominantnih dreves. Za analizo smo uporabili vzorce listja iz zgornjega dela krošnje na enakih ekspozicijah: v Murski šumi na ploskvah z nizko (M1) in visoko podtalnico (M2), v Krakovskem gozdu v gospodarskem sestoju (K1), gospodarjenem sestoju z manjšo sestojno gostoto, kjer so v letu 2002 izvedli posek 35 % lesne zaloge (blizu 500m^3) in je ostalo v sestoju od 40-45 dreves/ha in v pragozdnem rezervatu (K3). Meritve za izdelavo P/V krivulj smo izvedli v dvotedenskih obdobjih junija, julija in avgusta 2003 in 2004. Vzporedne meritve jutranjega vodnega potenciala (PWP) smo opravlili na istih mestih odraslega drevja in ploskvah obeh gozdnih kompleksov.

Potrdili smo razlike v osmotski komponenti med ploskvama v Murski šumi julija in avgusta 2003 in v Krakovskem gozdu med gospodarskim gozdom (K1) in pragozdom (K3). V letu 2004 so razlike in razmerja med ploskvami ostala enaka, absolutne vrednosti so bile manjše. Največjo stopnjo osmotske prilagoditve so pokazale vrednosti ploskve redčenega sestoja (K2) v primerjavi s ploskvijo (K1) in pragozdom. Osmotska prilagoditev hrastov pred redčenjem je bila v obeh ploskvah gospodarskega gozda enaka, po redčenju pa so drevesa, ki so ostala potrdila dobro prilagojen mehanizem prilagajanja vodnemu stresu kljub svoji starosti glede na neredčeno ploskev (K1), kjer takega fiziološkega odziva nismo potrdili.

6 References

6 Viri

ABRAMS, M. (1988) Sources of variation in osmotic potentials with special reference to North American tree species. Forest Science, 34, 4, pp. 1030-1046.

ARANDA, I., GIL, L., PARDOS, J. (1996) Seasonal water relations of three broadleaved species *Fagus sylvatica* L., *Quercus petraea* (Mattuschka) Liebl. and *Quercus pyrenaica* Wind.1 in a mixed stand in the centre of the

Iberian Peninsula. Forest Ecology and Management 84, p.219-229.

AUSSENAC, G. (1978) La sécheresse de 1976 : influences des deficits hydriques sur la croissance des arbres forestiers. Rev For Fr 30, 103-114.

BECKER, M., LEVY, G. (1982) Le dépérissement du chêne en forêt du Tronçais. Les causes écologiques. Ann Sci For 39, 439-444.

BREDA, N., COCHARD, H., DREYER, E., GRANIER, A. 1992. Water transfer in a mature oak stand (*Q.petraea*): seasonal evolution and effects of a severe drought.- Can. J. For. Res., 23, p 1136-1143.

CANNY, M.J. (1998) Transporting water in plants. Am. Sci. 86, p.152–159.

COCHARD, H., BREDA, N., GRANIER, A. 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism?. Ann. Sci. For. 53, 2-3, 197-206.

CORCUERA, L., CAMARERO, J.J., GIL-PELEGRÍN,E .(2002) Functional groups in *Quercus* species derived from the analysis of pressure–volume curves. Trees 16, p.465–472.

ČATER, M., SIMONČIČ, P., BATIČ, F. (1999) Pre-dawn water potential and nutritional status of pedunculate oak (Q*uercus robur* L.) in the north-east of Slovenia. Phyton (Horn), 1999, vol. 39, fasc. 4 (Spec. issue: "Eurosilva"), p. 13-22.

ČATER, M. (2003) Pedunculate oak (*Quercus robur* L.) crown defoliation-changes on permanent research plots. Ekológia (Bratisl.), 2003, 4, p. 430-443.

ČATER, M., BATIČ, F. (2006) Groundwater and light conditions as factors in the survival of pedunculate oak (*Quercus robur* L.) seedlings. European journal of forest research vol. 125, no. 4, 419-426.

DICKSON, R..E., TOMLINSON, S.T. 1996. Oak growth, development and carbon metabolism inresponse to water stress.- Ann. Sci. For. 53, 2-3, 181-196.

DREYER, E., BOUSQUET, F., DUCREY, M. (1990) Use of pressure volume curves in water relation analysis on woody shoots: influence of rehydration and comparison of four European oak species. Ann Sci For 47, p.285-297.

EPRON, D., DREYER, E. 1996. Starch and soluble carbohydrates in leaves of water-stressed oak saplings.- Ann. Sci. For., 53, 2-3, 263-268.

HANSON, A.D., HITZ, W.D. (1982) Metabolic responses of mesophytes to plant water deficits. Annu. Rev. Plant Thysiol., 33, p. 163-203.

HINCKLEY, T.M., DUHME, F., HINCKLEY, A.R., RICHTER, H. (1980) Water relations of drought hardy shrubs: osmotic potential and stomatal reactivity. Plant Cell Environ 3, p.131–140.

HOLBROOK, N.M., ZWIENICKI, M.A. (1999) FIELD, C.B. 1999. Embolism repair and xylem tension: do we need a miracle? Plant Physiol. 120:p.7–10.

JEFFERIES, R.L. (1981) Osmotic adjustment and the response of halophytic plants to salinity. Bioscience, 31, p. 42-46.

KRAMER, P.J. (1969) Plant and Soil Water Relationships: A Modem Synthesis. McGraw-Hill, New York, NY, USA.

LARCHER, W. (1995) Physiological plant ecology.- Ecophysiology and stress physiology of functional groups.- Berlin, Springer-Verlag, 506 p

METHY, M., DAMESIN, C., RAMBAL, S. 1996. Drought and photosystem II activity in two Mediterranean oaks.- Ann. Sci. For., 53, 2-3, 255-262.

NI, B.R., PALLARDY, S.G. (1991) Response of gas exchange to water stress in seedlings of woody angiosperms. Tree Physiol., 8., p. 1l-9.

OSONUBI, O., DAVIES, J.W. (1978) Solute accumulation in leaves and roots of woody plants subjected to water stress. Oecologia (Berl.) 32, p. 323-332.

PALLARDY, S.G. (1989) Hydraulic architecture and conductivity: an overview. In: KH Kmeb, H Richter and TM Hinckley (Ed), Structural and Functional Responses to Environmental Stresses: Water Shortage. SPB Academic Publishing bv,The Hague. pp. 3-19.

PARKER (1982) Seasonal changes in tissue water relations of three woody species of the *Quercus-Carya* forest type. Ecology 63, p. 1259-1267.

SCHOLANDER, P.F., HAMMEL, H.T., BRADSTREET, E.D., HEMMINGSEN , E.A. (1965) Sap pressures in vascular plants. Science 148, p.339–346 MORGAN, J.M., (1984) Osmoregulation and water stress in higher plants. Ann Rev Plant Physiol 35, p. 299-319.

TALBOT, A.J.B., TYREE, M.T., DAINTY, J. (1975) Some notes concerning the measurement of water potentials of leaf tissue with specific reference to *Tsuga canadensis* and *Picea abies*. Can J Bot 53, p.784–788.

TIMBALL, J., AUSSENAC, G. 1996. An overview of ecology and silviculture of indigenous oaks in France.-Ann. Sci. For. 53, 2-3, 649-661.

TOGNETTI, R., GIOVANNELLI, A., LONGOBUCCO, A., MIGLIETTA, F., RASCHI, A. 1996. Water relations of oak species growing in the natural CO2 spring of Rapolano (cental Italy).- Ann. Sci. For. 53, 2,475-485.

TRIBOULOT, M.B., FAUVEAU, M.L., BREDA, N., LABEL, S., DREYER, E. 1996. Stomatal conductance and xylem-sap abscisic acid (ABA) in adult oak trees during a gradually imposed drought.- Ann. Sci. For. 53, 2-3, 207-220.

TURNER, N.C., JONES, M.M. (1980) Turgor maintenance by osmotic adjustment: A review and evaluation. In: Adaptation of Plants to Water and High Temperature Stress (N.C. TURNER, P.J. KRAMER, eds), John Wiley and Sons, London, p. 87-103.

TYREE, M.T., COCHARD, H. 1996. Summer and winter embolism in oak: impact on water relations.-Ann. Sci.For. 53, 2-3, 173-180.

TYREE, MT, HAMMEL, H.T. (1972) The measurement of the turgor pressure and water relations of plants by the pressure-bomb technique.J.Exp.Bot, 23, p. 267-282.

VIVIN, S., GUEHL, J.M., CLEMENT, A., AUSSENAC, G. 1996. The effects of elevated CO2 and water stress on whole plant CO2 exchange, carbon allocation and osmoregulation in oak seedlings.-Ann. Sci. For. 53, 2-3, 447-459.

ZWIENICKI, M.A., HOLBROOK, N.M. (2000) Bordered pit structure vessel wall surface properties. Implications from embolism and repair. Plant Physiol. 123:1015–1020.