

## Diurnal and Seasonal Changes in Stem Radius Increment and Sap Flow Density Indicate Different Responses of Two Co-existing Oak Species to Drought Stress

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**Abstract** – Using continuous monitoring of stem radius combined with sap flow measurements we assessed the effects of environmental conditions on tree radial growth and water status of two co-existing oak species (*Quercus petraea* and *Quercus cerris*) at high resolution time in growing seasons of 2008 and 2009. The forest (95–100 yr) is situated in a xeric site in the transition zone between forested and forest-steppe regions in north-eastern Hungary, Bükk mountains (47°90'N, 20°46'E, elevation 320–340 m a.s.l.). Weather conditions in the growing season of 2008 (total rainfall 354 mm, mean daily temperature 17.0 °C) was less extreme than in 2009 (total rainfall 299 mm, temperature 17.9 °C). Rainfall strongly determined the course of radial growth increment in trees. Radial growth of trees was limited in 2009 due to the drought in spring. The maximum radial increment of both species was achieved three weeks earlier (4<sup>th</sup> week of June) than in 2008 (4<sup>th</sup> week of July). We used dendrometer monitoring data for estimation of stem (tree) water deficit ( $\Delta W$ ) by measuring water-related changes in stem radius (Zweifel et al. 2005). The magnitude of tree water deficit variation ( $\Delta W$ ) was always smaller in *Q. cerris* than in *Q. petraea*. In contrast, *Quercus cerris* always exhibited larger daytime averages and maxima of sap flow density. In August of 2009 when drought became severe there were larger increases in tree water deficit ( $\Delta W$ ) (50–55 %) in both species compared to July as it could be expected from the extent of decreases in sap flow density (24–28%). Our data suggested that due to the low SWC the transpiration was supported mainly from the inner water storage of trees during prolonged drought which resulted in high stem water deficit ( $\Delta W$ ).

**drought / forest/potential evapotranspiration / Quercus petraea / Quercus cerris / stem (tree) water deficit**

**Kivonat** – Két zonális tölgyfaj törzsnövekedésének és nedváraamlásának napi és szezonális dinamikája. A tanulmányban összefoglalt eredmények részét képezik a Bükk-hegységi Síkfőkút Project LTER kutatási terület (47°90'N, 20°46'E, tszf. 320–340 m) cseres-tölgyes erdőállományban folyó növény-ökológiai kutatási programnak. Vizsgálataink során folyamatos dendrometriás és nedváraamlás méréseket végeztünk a 2008 és 2009 évek vegetációs időszakaiban annak megállapítására, hogy a kocsánytalan tölgy (*Quercus petraea* (Matt.) Liebl.) és a csertölgy (*Quercus cerris* L.) radiális

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törzsnövekedésében és vízforgalmában az időjárási extrémítások milyen mértékű változásokat okoznak. A dendrometriás mérési eredmények azt jelzik, hogy a csapadék mennyisége és eloszlása döntően meghatározza a törzsek radiális növekedését mindkét fajnál. Minkét faj esetében kimutattuk, hogy a 2009 évi tavaszi aszály hatására a törzsek radiális növekedése három héttel korábban befejeződött és alacsonyabb értéket ért el a 2008 évi növekedéshez képest. A törzs radiális változásának a finom időfelbontású mérése a növekedési ütemen kívül lehetőséget nyújtott arra is, hogy az adatok alapján a törzsek (fák) vízdeficit értékeit ( $\Delta W$ ) is megbecsüljük, amelyhez Zweifel et al. (2005) módszerét használtuk fel. A két fafaj közül a vízdeficit a *Q. petraea* törzsében mindig szignifikánsan nagyobb amplitúdójú változásokat mutatott, mint a *Q. cerris* esetében, ami alapján az utóbbi fajnál nagyobb törzsbeli vízkészletre következtettünk. Ugyanakkor a nedváraamlás nappali középértéke és maximuma mindig a *Quercus cerris* esetében volt magasabb. 2009 augusztusában, erősen aszályos időszakban mindkét fajnál jóval nagyobb mértékben (50–55%-kal) emelkedett a fatörzsbeli vízdeficit a júliusi mérési eredményekhez képest, mint amit az ugyanezen időszakban mért nedváraamlás csökkenés mértéke alapján várnánk (24–28%). Ez azt sugallja, hogy a fák a tartósan aszályos periódusokban a belső, törzsbeli vízraktárakat hasznosítják a vízszállító pályák feltöltésére és a transzpiráció fenntartására.

**aszály / nedváraamlás / *Quercus petraea* / *Quercus cerris* / radiális törzsnövekedés / vízdeficit**

## 1 INTRODUCTION

Owing to climate change (IPCC, 2007) the future survival and sustainability of forest ecosystems has become of great concern (Jump et al. 2009, Mátyás 2010). For Carpathian basin climate projections predict a reduction in the total area of climate-zonal forests and the gradual shift „forward” of transition between forest and forest-steppe zones (Mátyás – Czimber 2004). Severe and recurring drought has been identified as major contributing factor to the recently accelerated tree decline and mortality in Europe (e.g. Jakucs et al. 1986, Gibbs – Greig 1997, Siwecki – Ufnalski 1998, Thomas et al. 2002).

In Hungary serious tree decline has been reported for the mixed stands of sessile oak (*Quercus petraea* (Matt.) Liebl) and Turkey oak (*Quercus cerris* L.) from the 80's (Jakucs et al. 1986). These forests represent one of the most important vegetation type in the Carpathian basin therefore tree decline has large economic and nature conservation consequences. Sessile oak suffered more drastic decline than Turkey oak in Hungarian forests as well as in whole Europe. Mortality of sessile oak varied with site conditions and became very serious in xeric margins of this forest type suggesting that climate change will threaten sessile oak very strongly. Simulation of future distribution of sessile oak by BIOMOD model (Thuiller 2003) projects that there will be a shift of its bioclimatic envelope as a result of climate change. On regional scale, analyses provided also a very pessimistic scenario for Hungary since the species may lose the majority of the distribution area by 2080 (Czúcz et al. 2011).

The objective of this work was to analyse the effects of climatic fluctuations on growth and water status of two co-existing tree species (*Quercus petraea* (Matt.) Liebl. and *Quercus cerris* L.) in two subsequent growing seasons, 2008 and 2009. More specifically we intended 1) to estimate the influence of environmental conditions on stem radius increment with high time resolution; 2) to assess drought related responses of tree water deficit for the two species; 3) to describe seasonal and diurnal course of sap flow density and its correlation with environmental factors.

## 2 MATERIAL AND METHODS

### 2.1 Study site and experimental trees

The study was carried out at Síkfőkút Project LTER forest site (47°90'N, 20°46'E, elevation 320–340 m a.s.l.), Bükk Mountains, north-eastern Hungary in summer of 2008 and 2009.

The site is covered by a mixed forest stand (95–100 yr) dominated by sessile oak (*Quercus petraea*) and Turkey oak (*Quercus cerris*) in the canopy layer. The soil of the site is a deep brown forest soil formed on miocenic pebble (Jakucs 1985). According to the current climatic conditions the site is close to the forest-steppe limit. The average annual rainfall of the past 30 years is 555 mm and the mean annual temperature is 10.3 °C at the site (Table 1). The growing season usually lasts from mid-April to mid-October. In the northern mountain region of Hungary the annual total of global radiation falls between 4300–4400 MJ m<sup>-2</sup> (Jakucs 1985). During the past decade extreme drought and heat-waves have appeared at the site in summer of 2003, 2007 and 2009.

The tree species composition of the stand was: *Quercus petraea* 46.9%, *Quercus cerris* 22.8%, *Carpinus betulus* 0.4%, *Acer campestre* 28.2%, *Acer tataricum* 0.9%, *Cerasus avium* 0.8%. Trees of oak species belong to the dominant and co-dominant crown classes, while other tree species represent intermediate and co-dominant crown classes of forest canopy.

For our study we selected one mature sessile oak and one Turkey oak (95–100 years old). Both trees represented the dominant crown class growing to uppermost position of the forest canopy (height of experimental trees was 20–22 m, DBH of the sessile oak tree was 29 cm, for Turkey oak 46 cm).

### 2.2 Measurements of environmental parameters

Weather conditions were monitored automatically by Hobo ProSeries RH&Temp sensor (Onset Computer Corporation, Pocasset, USA), and Hobo Micro Station (Onset Computer Corporation, Pocasset, USA) with external sensors (Rain gauge, PAR, atmospheric pressure, wind speed) during the study period. Weather data were recorded at every 30 min. at the top of a meteorological tower (25m above ground). Volumetric soil moisture content (SWC) was measured using ECH<sub>2</sub>O sensors (Decagon Devices, Pullmann WA, USA) within the upper 30 cm with 15 min sampling interval.

To assess the differences in the microclimatic conditions between vegetation seasons of 2008 and 2009 we calculated the cumulative daily mean temperature and cumulative rainfall. Cumulative daily mean temperature and rainfall data and course of soil moisture in 2008 and 2009 are presented in Figure 1. Due to the lack of measurements of global radiation, the Hargreaves-Samani temperature based method was used to estimate the the mean daily potential evapotranspiration (PET mm day<sup>-1</sup>) (Hargreaves – Samani 1982).

### 2.3 Sap flow measurements

Continuous sap flow measurements began at our site in growing season of 2009. Sap flow density (ml cm<sup>-2</sup> min<sup>-1</sup>) was measured with heat dissipation method developed by Granier (1985). An SF-G sensor (Ecomatik, GmbH, Dachau, Germany) was mounted on the northern side of tree stems to avoid direct solar heating and shielded with aluminum foil to minimize temperature fluctuations in the sapwood. The SF-G sensor consists of two identical needles with copper-constantan thermocouples and a special heating wire. The two needles were inserted 2 cm into the sapwood, one above the other, 15 cm apart. The upper needle was installed at a height of 1.5 m. The top needle was heated with constant energy supply (at 12V with 83 mA). The temperature difference between the two needles ( $\Delta T$ ) was the output signal of the sensor and used for calculation of sap flow density according to the formula by Granier (1985):

$$u = 0.714 * [(\Delta T_{\max} - \Delta T) / \Delta T]^{1.231},$$

where

$\Delta T$  is temperature difference between two needles;

$\Delta T_{\max}$  is the maximum value of  $\Delta T$  when sap flow can be considered as 0 during night.

SF-G Sensors were installed on March 26 2009 and monitoring of  $\Delta T$  was planned in 5 min interval till the end of October but there were some short periods during the growing season when unexpected errors (due to heavy rain events, animal damages etc.) disrupted the continuous measurement.

## 2.4 Measurements of tree stem radius changes and estimation of tree water deficit

Tree stem radius changes ( $\Delta r$ ) were monitored with automated DR dendrometers (Ecomatik GmbH, Dachau, Germany) with resolution up to 0.2 microns. The dendrometers were mounted at 1m above ground on north side of stem of one sessile oak and one Turkey oak tree. Continuous recording of stem radius changes began on June 6 2008.  $\Delta r$  was recorded in 10 min intervals.

A sensor fixed in a frame was installed to the measuring section of the stem after removal of the dead bark. Sensors were installed carefully to avoid damages to the living tissues below the dead bark. The course of  $\Delta r$  depends mainly on stem radial growth and fluctuation of water-storage. Other factors e.g. temperature and xylem-tension-related fluctuations may contribute only slightly (<10%) to  $\Delta r$  (Zweifel et al. 2005). From the course of  $\Delta r$  we estimated the changes in stem water-storage by using the algorithm suggested by Zweifel et al. (2005). We hypothesized that a rainfall event above 10 mm can induce stem hydration and increase of  $r$  to maximum. The difference between the trunk radius of maximum hydrated (normally after a rainfall event) state and actual hydration status was used for quantifying the degree of stem water deficit ( $\Delta W$ ) during a given period. This is also considered as a measure of water deficit in the whole tree and defined as tree water deficit (Hinckley – Lassoie 1981).

## 3 RESULTS

### 3.1 Weather and soil moisture conditions

Compared to the average weather conditions of the last 30 years (1978–2007), annual mean temperature was higher by 0.9–1 °C in 2008 and 2009 (*Table 1*).

The vegetation period of both study years was warmer and drier than the average. Summer of 2009 was extraordinarily hot and had one of the lowest total amounts of rain during the last decade (*Figure 1*). However, in 2009 the total annual rainfall did not differ from the 30 year average while in 2008 it was 56 mm lower (*Table 1*).

In 2009 there was a four-week period without rainfall during budburst in April which led to rapid decline of soil moisture content (*Figure 1*). The whole vegetation period of 2009 was drier and warmer than in 2008 with low volumetric water content. In 2009 the end of vegetation period was without rain events that caused large water deficits in the soil in September. During the vegetation period of 2008 the soil was wet in spring. Volumetric soil water content transiently decreased in May, but it increased in June and July due to frequent rains.

Table 1. Annual mean of air temperature ( $T$ ), mean daily air temperature of vegetation period ( $T_{04-10}$ ), annual total rainfall ( $P$ ) and total rainfall of vegetation period ( $P_{04-10}$ ) in 2008 and 2009. Long-term mean values of air temperature and rainfall were calculated for 1978–2007

	$T$ °C	$T_{04-10}$ °C	$P$ mm	$P_{04-10}$ mm
2008	11,3	17,0	499	354
2009	11,3	17,9	554	299
30-year mean (1978–2007)	10,4	16,5	555	393

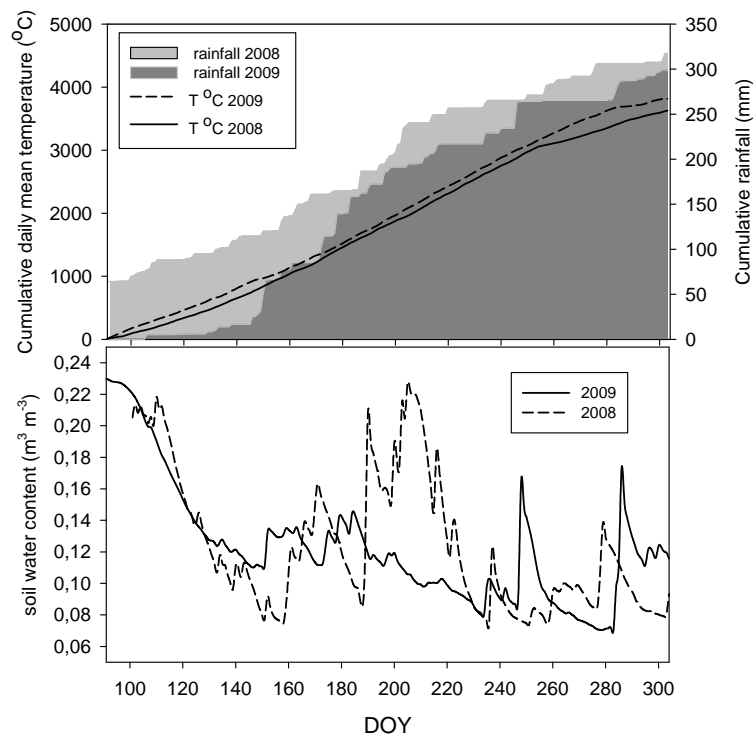


Figure 1. Cumulative values of daily mean air temperature, cumulative daily precipitation (upper figure) and volumetric soil water content (lower figure) during the growing seasons of 2008 and 2009 in the Síkfökút study area

### 3.2 Stem radius changes and variation in tree water deficit

Dendrometers were installed on tree stems on June 6 2008. We selected a three-month period between DOY158 and 248 in 2008 and 2009 for comparison of stem radius changes ( $\Delta r$ ). Although the course of  $\Delta r$  was different in 2008 and 2009, the stem radial increment did not change after DOY 248 in both years (Figure 2). DOY 158 is considered as reference day and  $\Delta r$  values show deviations from it.

The dendrometer data was set as 0 on the first day of this selected period. During the three-month period in 2009 there was only 750–850  $\mu\text{m}$  maximum increment for *Quercus petraea* 500–600  $\mu\text{m}$  for *Quercus cerris*. Stem radius stopped to increase by the first week of July 2009 and then only short-term fluctuations occurred due to the daily transpiration and rainfall events.

In 2008, however, both species showed three or four times larger stem radius increase in the corresponding period than in 2009 (Figure 2). In the corresponding period of 2008 the stem radius change was 2100–2300  $\mu\text{m}$  for *Quercus petraea* and 1800–2100  $\mu\text{m}$  for *Quercus cerris* in the three month period. In 2008 the stem radius showed increases till the end of July.

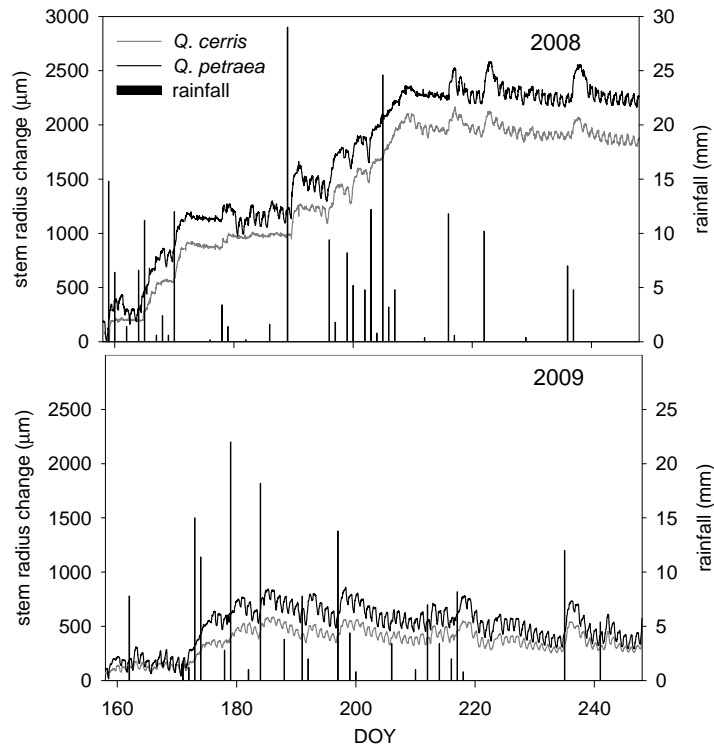


Figure 2. Temporal course of cumulative stem radius change ( $\Delta r$ ) for *Quercus petraea* (black line) and for *Quercus cerris* (gray line) and daily sums of rainfall in summer of 2008 and 2009. DOY 158 is considered as reference day and  $\Delta r$  values show deviation from it

The three-month long dendrometer data series were also used to estimate fluctuations in water status of tree stems. Seasonal variations in stem water deficit calculated by means of method suggested by Zweifel (2005) are presented in Figure 3.

The general seasonal course of  $\Delta W$  was similar for the two species in both years. Seasonal amplitude of stem water deficit differed in the two species, it was smaller for *Quercus cerris* than for *Quercus petraea*.

Variation of stem water deficit was, however, usually the most significant during dry periods and approached zero after heavy rain events. Even one-two week dry periods could induce rapid increases of tree water deficit depending on the soil water availability and VPD. In 2008 large stem water deficit developed within the period from DOY 175 to DOY 190 (4th week of June and 1st week of July) up to 250  $\mu\text{m}$  for *Quercus cerris*, and 500  $\mu\text{m}$  for *Quercus petraea* and between DOY 223 and DOY 236 up to 230  $\mu\text{m}$  and 420  $\mu\text{m}$  for *Quercus cerris* and *Quercus petraea*, respectively. In 2009 a long-lasting stem water deficit period appeared from DOY 200 to DOY 234 with 300 and 450  $\mu\text{m}$  maximum values of  $\Delta W$  for for *Quercus cerris* and *Quercus petraea*, respectively. There was only a short (3 days) interruption of this period when  $\Delta W$  of stem approached 0 in both species. The diurnal fluctuation of  $\Delta W$  were also different in the two species (Figure 3).

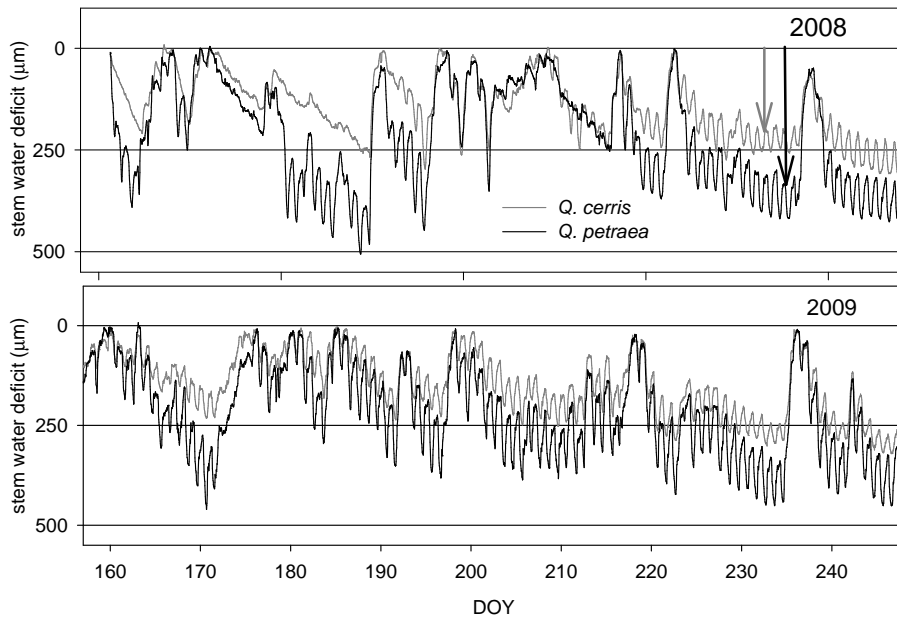


Figure 3. Variation in stem (tree) water deficit ( $\Delta W$ ,  $\mu\text{m}$ ) with time for *Quercus petraea* (black line) and *Quercus cerris* (gray line)

On most sampling days in 2008 both species showed lower diurnal amplitudes of  $\Delta W$  than in 2009. In 2008 diurnal amplitude of  $\Delta W$  reached 80–120  $\mu\text{m}$  in *Quercus petraea* and 40–80  $\mu\text{m}$  in *Quercus cerris*. In 2009 the diurnal variation of stem radius extended to 130–200  $\mu\text{m}$  in *Quercus petraea* and to 40–100  $\mu\text{m}$  in *Quercus cerris*.

### 3.3 Variation of main daytime sap flow density and correlation with PET in summer of 2009

In the second half of the vegetation period of 2009 we experienced severe drought at the site. During the experimental period from DOY 209 to DOY 283 mean daytime sap flow density ranged between 0.11 and 0.04  $\text{ml cm}^{-2} \text{min}^{-1}$  in *Quercus cerris*, and 0.07 and 0.02  $\text{ml cm}^{-2} \text{min}^{-1}$  in *Quercus petraea*. During the same period the daily PET changed between 12 and 4  $\text{mm day}^{-1}$ .

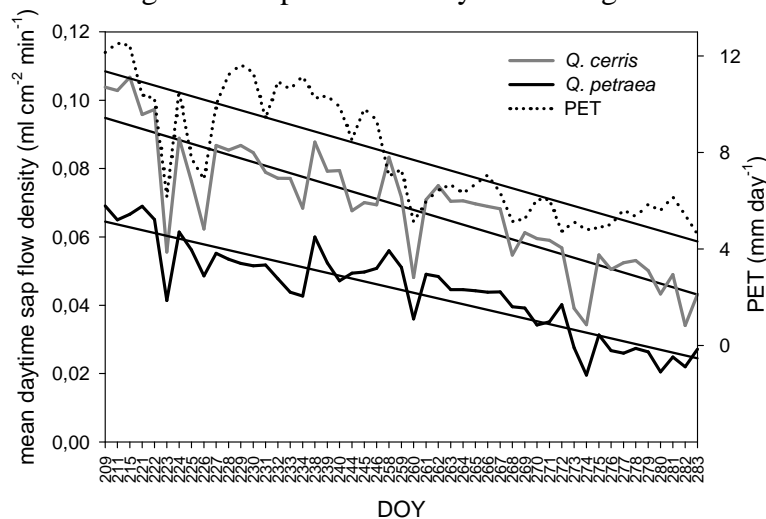


Figure 4. Daytime mean sap flow density of *Quercus petraea* (black line) and *Quercus cerris* (gray line) and potential evapotranspiration estimated by Hargreaves-Samani temperature based method (Hargreaves-Samani 1982) during the experimental period from DOY 209 to DOY 283. Rainy days are excluded from the data set

A general decreasing trend of mean daytime sap flow density was observed for both species as the drought proceeded in August and September (Figure 4). Analysis of a dataset from this period (50 days after exclusion of rainy days) showed that the daytime sap flow density of both species changed in close positive correlation ( $P < 0.01$ ) with PET which also showed declining trend in the second part of growing season. The correlation was closer for *Q. petraea* ( $R^2 = 0.6248$ ) than for *Q. cerris* ( $R^2 = 0.7410$ ).

### 3.4 Diurnal course of sap flow density

From the continuous sap flow measurements of 2009 we have selected days from two characteristic periods to assess the relationship between sap flow density and environmental conditions at daily scale.

- i) DOY 209, DOY 211 and DOY 215 represent sunny days in a moderately rainy period with small rains on DOY 210 (1 mm), DOY 212 (7mm) and DOY 214 (3.4mm), decreasing SWC (from 0.110 to 0.099  $\text{cm}^3 \text{cm}^{-3}$ ), high daytime VPD values ( $\text{VPD}_{\text{max}}$  3–4 kPa) and light intensity ( $\text{PPFD}_{\text{max}}$  1800–1900  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). There were only two small rains ( $< 4$  mm) rain during the previous 10 days (Figure 5).
- ii) DOY 231, DOY 232 and DOY 233 in the driest period of summer with SWC 0,080–0,083  $\text{cm}^3 \text{cm}^{-3}$ , high daily VPD ( $\text{VPD}_{\text{max}}$  2.9–3.6 kPa) and PAR ( $\text{PPFD}$  1700–1800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). There was no rainfall event in the previous 10 days (Figure 6). This period represented typical stage of the drought stress.

The magnitude of diurnal sap flow amplitude depended significantly on the environmental conditions on selected days and decreased as the drought stress proceeded on sunny and hot days (DOY 209, 211 and 215) of a moderately rainy period in July, the mean SWC value on the selected three days reached 0.10  $\text{cm}^3 \text{cm}^{-3}$ . The low SWC suggests that in July a significant depletion of soil water reserves occurred and small rains were not enough for soil refilling. Comparing with other periods of growing season both tree species exhibited relatively high stem water deficit on these days (Figure 3).

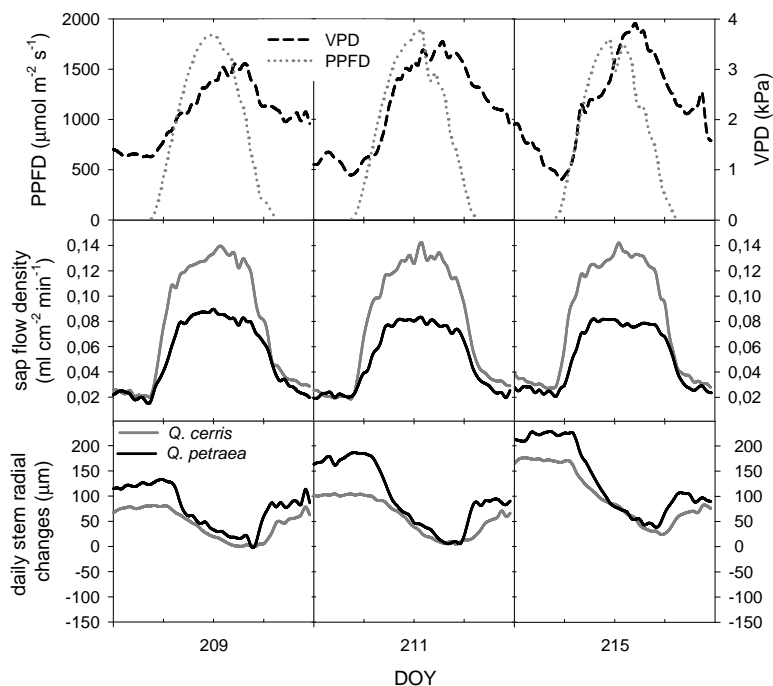


Figure 5. Diurnal course of VPD, light intensity (PPFD) and sap flow density and daily stem radial changes of *Quercus petraea* and *Quercus cerris* on sunny days of a moderately rainy period in July 2009



On DOY 209–Doy 215 the mean daily stem water deficit ( $\Delta W$ ) was 169  $\mu\text{m}$  for *Q. cerris* and 251  $\mu\text{m}$  for *Q. petraea* (Figure 3). Between the two selected periods sap flow density of both tree species was the highest on these days. The daytime mean sap flow was 0.10  $\text{ml cm}^2 \text{min}^{-1}$  in *Q. cerris* and 0.066  $\text{ml cm}^2 \text{min}^{-1}$  in *Q. petraea*. The daily maximum of sap flow was relatively high and approached 0.14  $\text{ml cm}^2 \text{min}^{-1}$  for *Q. cerris* and 0,09  $\text{ml cm}^2 \text{min}^{-1}$  for *Q. petraea* (Figure 5). VPD was very high on these days and showed daily maximum between 3.1 and 3.9 kPa. Sap flow density was in close correlation with VPD but showed a maximum earlier during the day. The stem radius reached maximum in the morning (between 6 and 8 a.m.) and minimum values in the afternoon (between 4 and 6 p.m.). Temporal appearance of minimum was closely related to the maximum of VPD.

In 2009 a progressive drought appeared from the first week of August which lasted almost for the whole month and was interrupted only by short rain events (Figure 1). SWC reached its minimal value (0.0819  $\text{cm}^3 \text{cm}^{-3}$ ) in this month considering the whole summer (Figure 1). On the three selected representative days of drought period (DOY 231–233) the daily maximum of sap flow was low in both tree species (0.101  $\text{ml cm}^2 \text{min}^{-1}$  and 0.064  $\text{ml cm}^2 \text{min}^{-1}$  (Figure 6). These sap flow density values were 28 % (*Q. cerris*) and 24 % (*Q. petraea*) lower than in July (Figure 5).

*Q. cerris* exhibited very similar diurnal course of sap flow density as in July in correlation with PPFD and partly with VPD too. While *Q. cerris* showed maximum sap flow density at midday, *Q. petraea* had a short maximum of sap flow density in the morning (at VPD 2–2.5 kPa) followed with a gradual reduction later on the day. The amplitude of diurnal variation in the stem radius was higher in *Q. petraea* than in *Q. cerris*.

Stem water deficit ( $\Delta W$ ) was 55 % (*Q. cerris*) and 49 % (*Q. petraea*) larger were deduced than in July. Mean daily value of  $\Delta W$  was 263  $\mu\text{m}$  for *Q. cerris* and 374  $\mu\text{m}$  for *Q. petraea* (Figure 3) suggesting the reduction of stem water storage due to the drought.

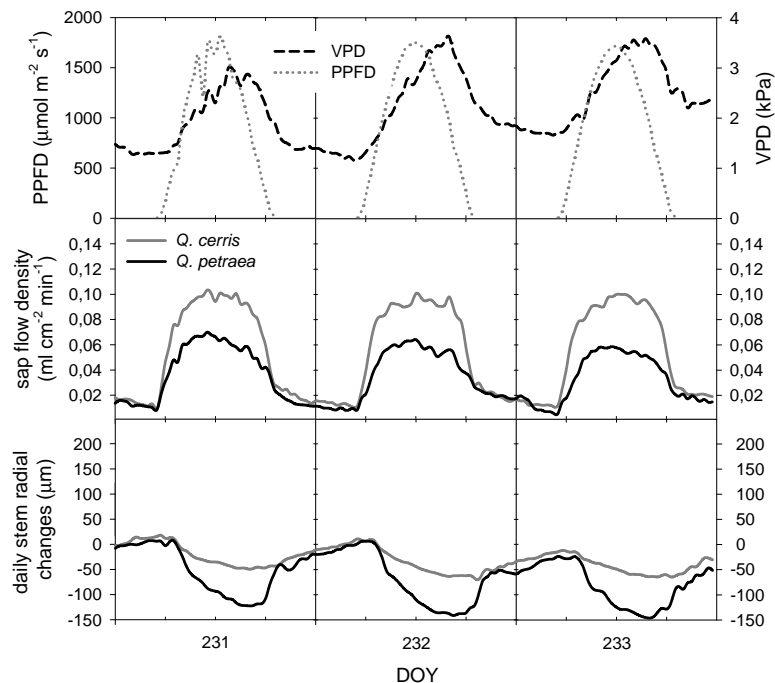


Figure 6. Diurnal course of VPD, light intensity (PPFD) and sap flow density and daily stem radial changes of *Quercus petraea* and *Quercus cerris* on sunny days during the drought in August 2009

#### 4 DISCUSSION

At the study site the temporal course of stem radial changes ( $\Delta r$ ) were analyzed during the period from 6 June till 15 September presuming different temporal growth dynamics of both species in 2008 and 2009. Rainfall strongly determined the course of radial growth increment in both species.

Due to the extreme environmental conditions in spring of 2009, the radial growth of trees was strongly limited by drought and the maximum radial increment of both species was reached three weeks earlier (by end of June) than in 2008 (by end of July). We suggest that the extreme drought in spring of 2009 combined with high temperature forced the trees to allocate carbohydrates to belowground carbon sinks to provide water and nutrients for shoot growth. Allocation of carbohydrates for producing fine roots when rainfall was low and SWC reduced rapidly could be a main cause for reduced growth rate of stem in the investigated period in 2009. Former studies suggest that carbohydrate supply to mycorrhiza might also contribute significantly to the switch of allocation pattern in trees under drought stress (Nehls et al. 2007).

At our site *Quercus petraea* exhibited larger stem increment during the experimental period of both years compared to *Quercus cerris*. The short-term fluctuations of  $\Delta r$ , however, were smaller in *Q. cerris* than in *Q. petraea*. This suggested that *Q. cerris* might have larger water storage in the trunk available for transpiration, as proposed by former studies on sap flow measurements (Tognetti 1996). Temporal course of stem (tree) water deficit also reflected that the two species might differ in water storage in the trunk. The magnitude of tree water deficit variation ( $\Delta W$ ) estimated from dendrometer monitoring data by measuring water-related changes in stem radius was always smaller in *Q. cerris* than in *Q. petraea*. In August of 2009 when drought became severe, increases (50–55 %) in tree water deficit ( $\Delta W$ ) of both species compared to July were larger as expected from the extent of decreases in sap flow density (24–28%). Water status including transpiration rate of trees is strongly determined by stomatal regulation (Zweifel et al. 2001, Gao et al. 2002). Therefore a strong stomatal influence on tree water deficit can also be postulated. Our data suggested that due to the low SWC the transpiration was supported mainly from the inner water storage of trees during prolonged drought which resulted in high stem water deficit (Figure 3).

Similar seasonal course of sap flow density was found for the two tree species, but *Quercus cerris* always showed higher sap flow density than *Quercus petraea*. In the regulation of sap flow, stomata play pivotal role. With their help water demand of trees can continuously be adjusted to the actual water availability (McDowell et al. 2008). Under decreasing SWC conditions by August, stomatal regulation became important in controlling the transpiration of both species. There was a decline in maximum daytime sap flow density during the drought period in August compared to that of July that can be interpreted as the consequence of stoma closure in the whole crown of both species. When trees experience very low SWC and high evaporation demand, the sap flow tends to be more and more controlled by stomata.

Stoma closure is the most efficient reaction to daily and seasonal water shortage. By closing their stomata, plants avoid harmful dehydration, although this goes at the expense of photosynthesis assimilation due to the limited uptake of  $\text{CO}_2$  (Mészáros et al. 2007). However, closing of stomata during daytime for long periods may induce carbon starvation of trees and affect their growth and competitive ability (Bréda et al. 2006, McDowell et al. 2008).

Concerning sap flow density the two tree species responded differently to the drought. In this period only *Quercus cerris* could maintain a regular diurnal pattern of sap flow density (and transpiration) (DOY 231–233, Figure 6) although at reduced maximum values.

Maximum sap flow density of *Q. petraea* gradually shifted back from midday by 2–4 hours to the morning on dry and hot days. This suggests the strengthening of dehydration-induced stomatal control over the light dependent stomatal regulation is in good agreement with reports on mature trees of other forest tree species (Aranda et al. 2000, Gartner et al. 2009).

Despite low SWC and high VPD, *Q. cerris* exhibited 38 % higher mean daytime sap flow density than *Q. petraea*. During the same period 42 % lower stem water deficit was estimated for *Q. cerris* than for *Q. petraea*. Such differences in water relations between the two co-existing species have significance in relation to competition under changing climate. This is clearly demonstrated by the shift of dominance conditions at the investigated site (Kotrocó et al. 2007).

## 5 CONCLUSIONS

Using continuous monitoring of stem radius changes combined with sap flow measurements at high time resolution we concluded that the two co-existing species respond differently to drought. Stem (tree) water deficit deduced from dendrometer measurements and temporal course of sap flow density can be used for assessing drought stress and describing inter-specific differences in tolerance and stress coping mechanisms.

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