

Leaf Growth and Photosynthetic Performance of Two Co-existing Oak Species in Contrasting Growing Seasons

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Abstract – Ecophysiological investigations of *Quercus petraea* and *Quercus cerris* were performed at the Sikfőkút research site in the dry and humid growing seasons of 2003 and 2004. The results suggested that leaf growth and the photosynthetic apparatus of *Q. petraea* exhibited higher sensitivity to drought in 2003 than that of *Q. cerris*. In leaves of *Q. petraea*, chlorophyll content showed larger inter-annual and within-canopy variability than in those of *Q. cerris*. Fully developed leaves of *Q. petraea* showed lower SLM which indicated higher leaf cell wall elasticity allowing them to maintain a water spending strategy, while high specific leaf mass (SLM) values reflected a water saving strategy for *Q. cerris*. Water use efficiency of *Q. cerris* was higher than in the case of *Q. petraea*, which may provide an advantage for this species in dry periods. In the contrasting years the final leaf area and leaf mass of both species were determined by the amount of rainfall and temperature conditions during the period of early exponential phase of leaf growth. As indicated by the low values of the Fv/Fm chlorophyll fluorescence parameter the photosynthetic apparatus of both species exhibited high susceptibility to abiotic stress factors in early spring. A large VAZ cycle pool indicated that zeaxanthin dependent heat dissipation was the main contributor to photoprotection of photosynthetic apparatus in young leaves but in fully developed leaves the relatively high light saturated ETR and low P_{max} as well as the maintenance of high Fv/Fm even in severe dry periods reflected the potential involvement of photorespiratory electron transport in photoprotection of both species in summer. Drought in 2003 may have resulted in serious depletion of dry matter reserves influencing the vitality of trees in following year. *Q. petraea* showed lower photochemical activity in the successive vegetation period after the dry year than *Q. cerris* which suggested lower tolerance to drought in the long term.

oak / drought / leaf growth / photosynthesis / photochemical efficiency of PSII

Kivonat – Cseres-tölgyes fajoknak levélnövekedése és fotoszintetikus teljesítménye kontrasztos időjárású években. A síkfőkúti cseres-tölgyes erdőállományban végzett vizsgálatok eredményei alapján megállapítható, hogy a kocsánytalan tölgy levélnövekedése és fotoszintetikus apparátusa nagyobb klimatikus érzékenységet mutat, mint a csertölgyé. A kocsánytalan tölgy esetében a klorofill-tartalom nagyobb évek közötti eltérést, és klimatikus változékonyságot mutat, mint a csertölgyénél. A kocsánytalan tölgy kisebb SLM értékekkel jellemezhető, mint a csertölgy, ami az előző fajnál nagyobb, az utóbbinál pedig kisebb sejtfal elasztikussággal társul. Az SLM és a WUE alapján

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megállapítható, hogy a *Quercus petraea* vízpazarló stratégiával, a *Quercus cerris* inkább vízmegőrző stratégiával rendelkezik. A két tölgyfaj fájnak adott vegetációs periódusban kifejlődő végleges asszimiláló lombfelületét és tömegét a levélnövekedés exponenciális fázisában uralkodó hőmérséklet és csapadékviszonyok nagymértékben befolyásolják. A lombfakadáskor és a levélnövekedés idején fellépő aszálynak nemcsak a levélnövekedés üteme, hanem a fák egész évi produkciója szempontjából súlyos következménye lehet. Nem csak a szerves anyag produkciójuk és a következő évi fiziológiájukat is meghatározó szerves anyag raktár csökken, hanem a fák legyengült állapotba kerülnek és a károsítókkal szemben is fogékonyabbá válnak. Mindkét tölgyfajra jellemző, hogy a fotoszintetikus apparátus a tavaszi időszakban nagy sérülékenységet és abiotikus stressz-tényezőkkel szembeni érzékenységet mutat. A nagy VAZ ciklus pigment készlet azt jelzi, hogy a fiatal levelek fényvédelmében a zeaxantin akkumulációval kapcsolódó hő disszipáció a meghatározó folyamat. A kifejllett levelekben a magas ETR ellenére alacsony P_{max} , és a száraz periódusban is magas Fv/Fm arra utalnak, hogy nyáron a xantofill ciklus mellett mindkét fajnál fontos szerepet kap a fotorespiráció a fényvédelemben. Az aszályos évet követő vegetációs időszakban a kocsánytalan tölgnél jelentkező alacsonyabb fotokémiai aktivitás a csertölgyhöz képest a vitalitás nagyobb mértékű gyengülését jelzi.

tölgy / aszály / levélnövekedés / fotoszintézis / PSII fotokémiai hatékonysága

1 INTRODUCTION

Numerous current scenarios on future climate change in Central Europe predict elevated temperatures and simultaneous reduction of rainfall in growing seasons which will increase the frequency and duration of summer drought (IPCC 2001). The reduced soil water availability as the main limiting factor for trees may have an adverse influence on the abundance and biomass production of European broad-leaved forests. There are several signs that climate change has already resulted in a shift of distribution and/or vigour of natural vegetation and further consequences are also forecast (Geßler et al. 2007). Climatic change and prolonged summer drought stress have been suggested as major contributing factors to the decline of central European forests in recent decades (Jakucs et al. 1986, Mészáros et al. 1993).

Severe summer drought such as that which occurred in 2003 may have long-term consequences for the forest condition by making the trees susceptible to other abiotic and biotic stresses appearing simultaneously or in subsequent growing seasons.

The climate projections for Hungary predict a reduction in the total area of natural climate-zonal forests and a gradual shift of transition between forest-steppe and forest zones (Mátyás – Czimmer 2004). The analyses showing the close relationships between the decline of health condition of zonal forest trees and the summer water shortage of their habitats have strengthened such predictions (Berki – Rasztovits 2004). Longer drought periods are expected to affect very seriously the tree species and forests occurring in transitional habitats in the North Hungarian Central Range, especially the mixed stands of Turkey oak (*Quercus cerris*) and sessile oak (*Quercus petraea*). A massive decline of oak (mostly sessile oak) has also been reported for forests of transitional habitats (Jakucs et al. 1986).

Although the climatic requirements of *Q. petraea* and *Q. cerris* have been well described on the basis of distribution pattern, the information on physiological traits and mechanisms determining the organic matter production and tolerance to fluctuations of weather and soil water availability are still lacking. For that reason the aim of this study was to characterise the physiological traits of *Q. petraea* and *Q. cerris* naturally co-occurring in a mixed forest stand by monitoring the fluctuation of leaf growth parameters and the functioning of photosynthetic apparatus within the canopy. Special focus has been on physiological responses of the two oak species to one of the most extraordinary droughts recorded for Hungary, which was experienced during the summer of 2003. Ecophysiological measurements performed during growing season of the humid year 2004 served as the reference of those in the dry year 2003.

Seasonal investigation of leaf physiological traits in an extreme growing season may provide an explanation for the differences in tolerance to environmental constraints and competitive abilities of co-existing tree species. This information may also be useful for predicting the effects of climate change on climate-zonal species and for modelling responses of forests to environmental stresses.

2 MATERIALS AND METHODS

2.1 Site conditions

The investigations were performed in the Sikfőkút long-term ecological research site established in 1972 in the Bükk Mountains, North Hungarian Central Range (Jakucs 1985). The site is situated at 320-340 m above sea level and is covered by a 85-90 year-old stand of sessile oak- Turkey oak forest community. From the start of the Sikfőkút project the forest stand has been untouched. Based on an average of 50 years the mean annual temperature is 9.9°C and the annual precipitation is 6.1 mm. The bedrock is miocenic grebble and the soil is deep brown forest soil.

The investigations were carried out in a 50 m x 50 m quadrat of the central 1 ha area of the site where a 25 m tower was built at the start of the long-term project for meteorological records and vegetation sampling. At this location the present composition of the tree layer consists of 84% *Q. petraea* and 16% *Q. cerris*. A substantial decline of sessile oak has occurred at the site since the 1980s which has resulted in drastic thinning of the tree layer, appearance of large gaps and gradual alteration of the vertical and horizontal dominance pattern of the forest stand (Mészáros et al. 1999). Reports on temperature, light conditions and soil moisture content have revealed drastic changes in microclimate within the interior of declining forest stand (Antal et al. 1997).

Compared to records from the early 1970s the present number of *Q. petraea* trees in the site is 60% lower. *Q. cerris* has also suffered a reduction in the number of individuals but only by 20%. (Koncz et al. 2005). Repeated field surveys have indicated an increase in the basal area of individual trees in both species (Mészáros et al. 2007) as compared to the period before decline (Jakucs 1985), but it was higher in *Q. cerris* (Table 1). However, when the present basal area of trees is calculated for 1 ha, *Q. petraea* oak shows a 57% decrease in total basal area, while *Q. cerris* exhibited a moderate increase (Koncz et al. 2005).

Table 1. Basal area of two tree species in the Sikfőkút forest in 1974 (Jakucs 1985) and in 2003

Species	Mean basal area of tree canopy (m ²)		Degree of change (%)
	1974	2003	
<i>Qurrus petraea</i>	11.1	12.6	+13.6
<i>Quercus cerris</i>	13.8	18.2	+32.6

In the present state of the forest stand the shrub layer in the canopy gaps show a similar structure (Mészáros et al 1999) to that reported for the edge of the forest (Mészáros et al. 1981). *Acer campestre* and *Acer tataricum* exhibited very intense growth and have formed a second, lower canopy layer of the stand. In spite of the opened canopy layer, regeneration of both oak species is rather poor and the cover of the herb layer is low. The latter observations, together with the large extent of oak decline, suggest that the habitat can be considered as a transitional one for sessile oak - Turkey oak forest (*Quercetum petraeae-cerris*).

2.2 Measurements of weather conditions

The investigations were performed during the 2003 and 2004 growing seasons. The weather conditions (temperature, relative humidity, rainfall, and photosynthetically active radiation, PAR) were monitored by means of automatic sensors with dataloggers (Onset Co., USA) located at the top of the meteorological tower. The processing of records was performed by BoxCar 4.3 Pro software. The soil moisture content was measured using the gravimetric method on sampling days. Soil samples were taken from the top 300 mm layer at three points of the study quadrats near the sample trees. To prevent water loss soil samples were placed in plastic bags prior the measurements.

2.3 Measurements of ecophysiological traits

Leaf samples were collected regularly during the growing seasons. In spring and early summer the interval between samplings was shorter (1-2 weeks) than later (3-4 weeks). Four trees of each species growing close to the meteorological tower and less than 10 m apart from each other were selected at random for measurements. Small twigs were cut from the sun and shade layers of sample trees with telescopic shears from the tower or from the ground.

Leaf area was measured by an AreaScope leaf area meter (developed at the Department of Botany, University of Debrecen), leaf dry mass was measured after drying at 85°C. Leaf discs taken for biochemical analysis were frozen in liquid nitrogen and kept at -70°C until processing.

Chlorophyll fluorescence parameters (F_v/F_m , $\Delta F/F_m'$) were measured with a PAM 2000 fluorometer (WALZ, Germany) (Schreiber et al. 1994). F_v/F_m was measured after 1 h dark acclimation. $\Delta F/F_m'$ of light acclimated samples was used for calculation of electron transport rate, $ETR = \Delta F/F_m' \times PPFD \times 0.84 \times 0.5$ as suggested by Genty et al. (1989).

Photosynthetic pigment composition of leaves was measured in 80% acetone extract. Chlorophylls were determined by the spectrophotometric method (Shimadzu UV/VIS spectrophotometer) using the equations of Wellburn (1994). Carotenoid composition was measured by reversed phase HPLC method (UV/VIS HPLC, Jasco, Japan), with application of zeaxanthin as standard.

Leaf gas exchange parameters were assessed using a LA2 infrared gas analyser (ADC, UK) under ambient air and saturating light conditions supplied by a portable lamp. Ratio of light-saturated photosynthesis (P_{max}) to transpiration rate (E) was used for estimation of water use efficiency (WUE).

3 RESULTS

3.1 Weather conditions

Concerning the weather conditions the two study years were completely different, especially in the seasonal distribution and the total amount of rainfall and temperature fluctuations (Figure 1). In 2003, after a dry winter period the precipitation was 30% less during the vegetation period than in 2004. The mean daily air temperature was significantly higher in the growing season of 2003 than in the respective period of 2004.

In 2003 low values of Gaussen-Bagnouls' xerotherm index (Table 2) indicated persisting drought for spring and early summer, the main period of canopy development.

The soil moisture content was low in the spring of 2003 and fell to 15% (f.m.) in June and remained around this value till the end of growing season (Figure 2). Although there was a large amount of rainfall in July it could not moderate the soil water deficit. After the drought

of 2003 the soil water budget did not fully recover during the winter months and low soil moisture occurred again in the topsoil during summer of 2004.

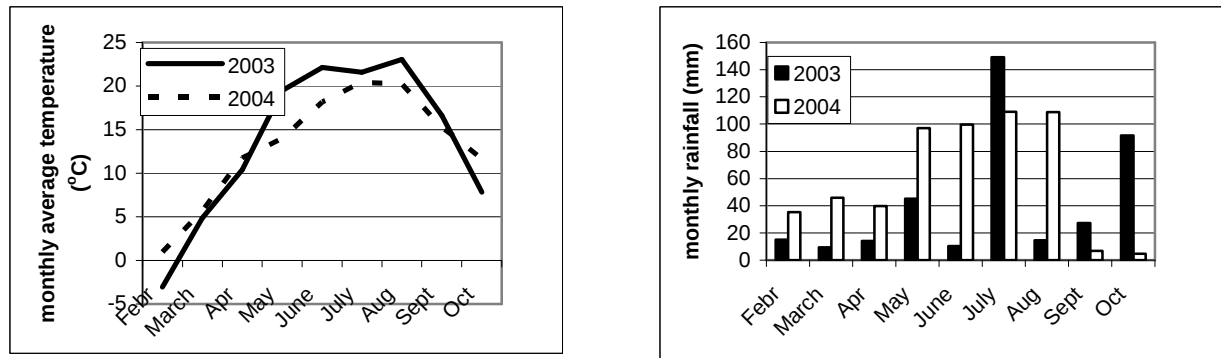


Figure 1. Monthly averages of daily mean temperature and monthly sums of rainfall in growing seasons of 2003 and 2004 at Síkfölkút Research Site

Table 2. Values of Gaussen-Bagnouls' xerotherm index in growing seasons of 2003 and 2004. Bold values indicate the ecologically dry months

	2003	2004
March	0.599	2.684
April	0.333	1.119
May	0.774	2.328
June	0.156	1.629
July	2.301	1.998
August	0.209	1.794
September	0.548	0.353

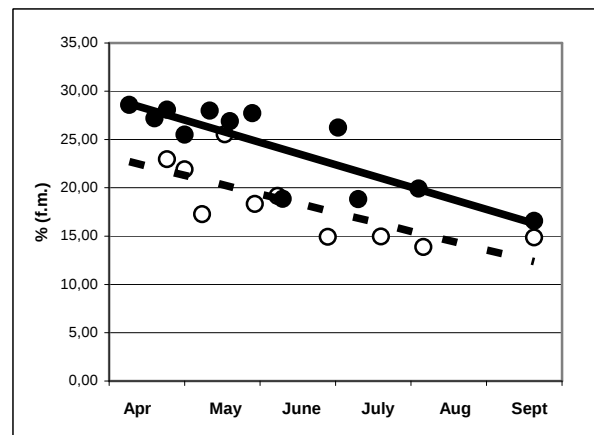


Figure 2. Soil moisture content (0-30 cm) in growing seasons of 2003 and 2004 at Síkfölkút Research Site

3.2 Leaf growth

Q. petraea showed larger inter-annual and within-canopy variations in area and mass of fully developed leaves than *Q. cerris* (Figure 3). In the upper canopy of both species leaf area was similar in different growing seasons but in shade layer it was significantly larger in the humid 2004 than in 2003.

The persisting drought in 2003 resulted in a large reduction of leaf mass in both canopy layers of *Q. petraea*. *Q. cerris* showed slight inter-annual changes in leaf mass; only the mass of fully developed shade leaves was smaller in 2003 as compared to 2004. The differences in leaf growth between the canopy layers between species and years appeared clearly in the exponential phase of leaf development (Figure 4). The drought in the spring and early summer of 2003 resulted in smaller slopes of growth curves of leaf mass in both canopy layers of both species than in 2004. The specific leaf mass (SLM) of expanded sun and shade leaves of *Q. petraea* was 15-20% lower in 2003 (Figure 3). This reflected decreases of density and/or thickness of leaf. In case of *Q. cerris* the inter-annual variation of SLM was less (3-10%).

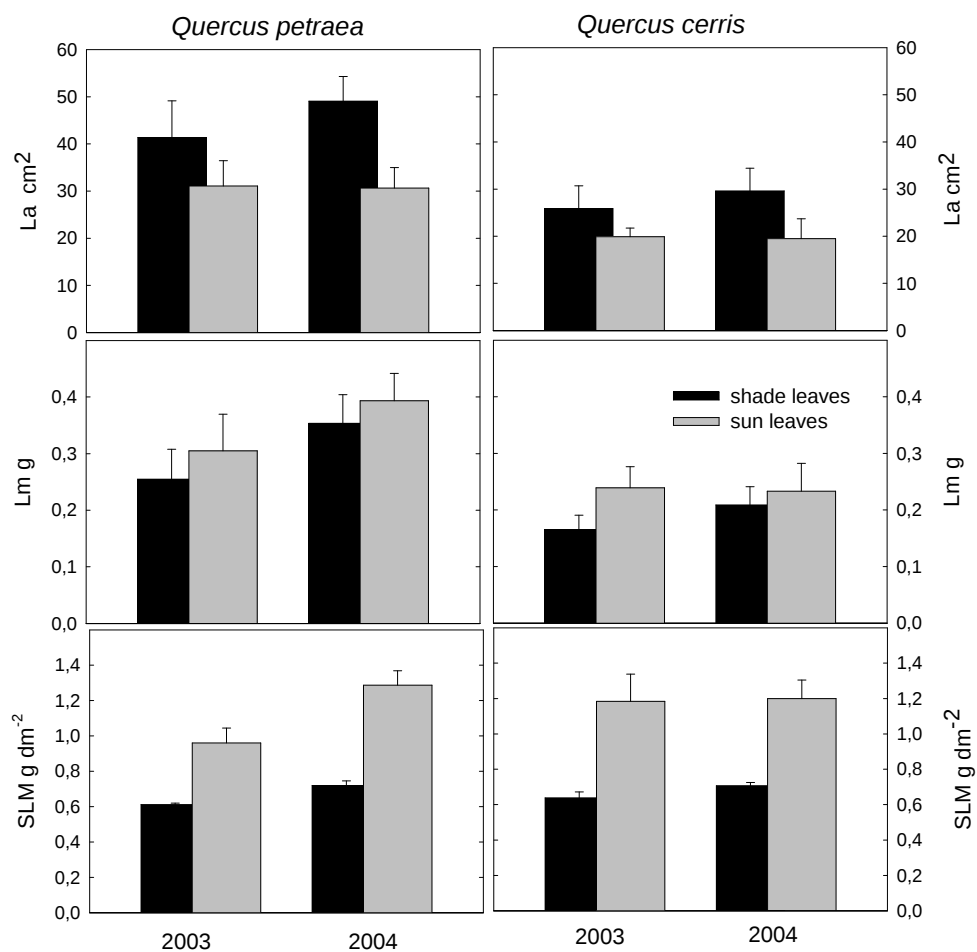


Figure 3. Leaf area, leaf mass and specific leaf mass (SLM) of fully developed sun and shade leaves of *Quercus petraea* and *Quercus cerris* in 2003 and 2004.

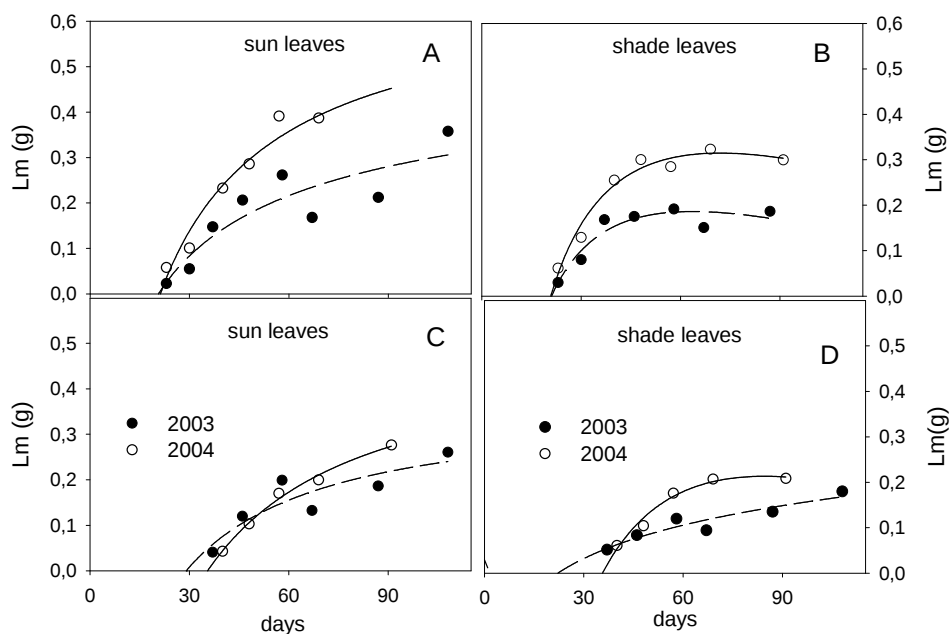


Figure 4. Exponential phase of leaf mass increment in sun and shade canopy layers of *Quercus petraea* (A and B) and *Quercus cerris* (C and D). 0 day indicates 1 April.

3.3 Photosynthetic pigments

Leaf chlorophyll content per unit dry matter increased from spring until summer in sun and shade leaves of both species (*Figure 5*). Carotenoid content per unit dry matter was higher in spring than in summer. Fully developed leaves in both canopy layers of sessile oak contained lower concentrations of all pigment groups in 2003 than in 2004. The chlorophyll content of leaves of Turkey oak was similar in different years but total carotenoid content was lower in 2003.

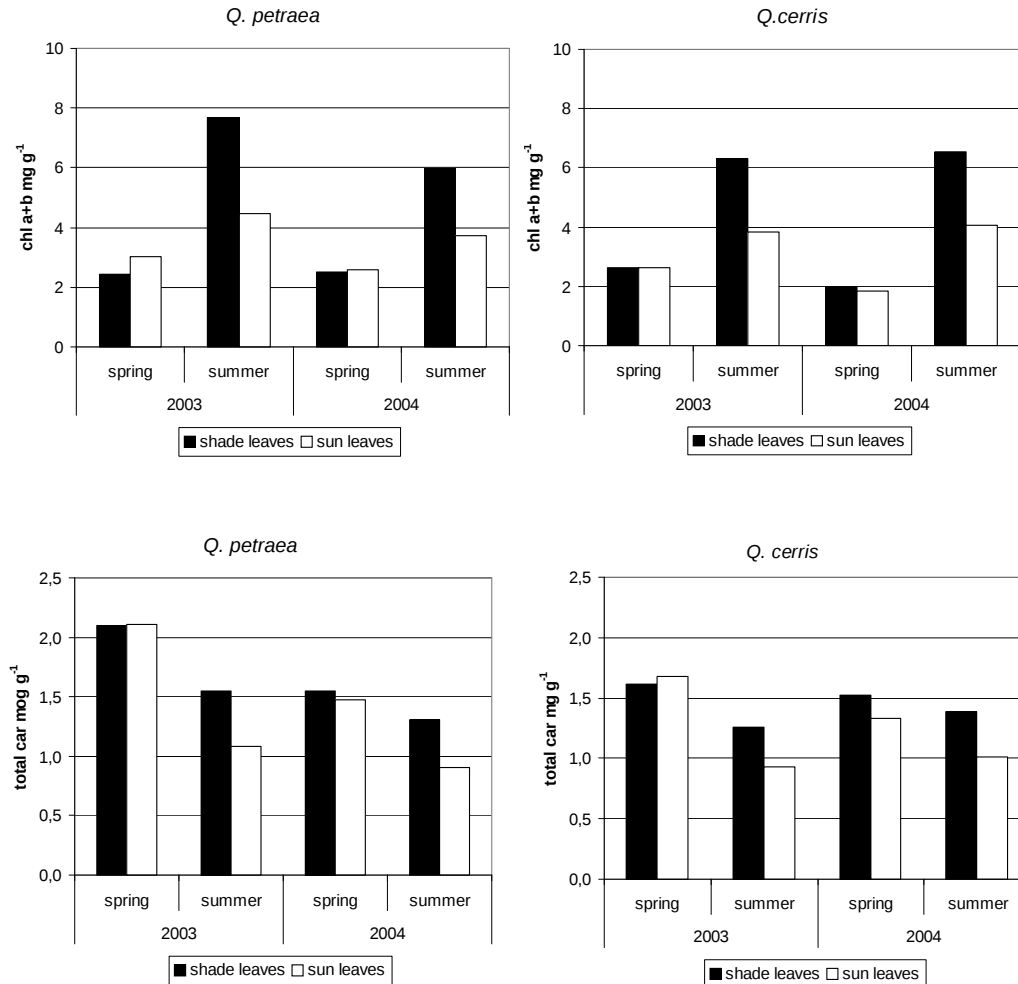


Figure 5. Chlorophyll and total carotenoid content (mg g⁻¹ dry matter) in sun and shade leaves of Quercus petraea and Quercus cerris in growing seasons of 2003 and 2004.

Similarly to the carotenoid content per unit of dry matter, a significant reduction in the total carotenoid pool expressed on a chlorophyll basis (mmol mol⁻¹ chlorophyll a+b) was also observed in summer (*Figure 6*). Although sun leaves contained less carotenoids per unit dry matter than did shade leaves (*Figure 5*) similarly to chlorophylls the total carotenoid pool per unit of chlorophyll was higher in sun leaves (*Figure 6*).

The differences in this biochemical trait between the canopy layers were larger for *Q. petraea*. The variation of carotenoid pool in the early and late growing seasons appeared to be closely correlated with the changes in the total content of pigments taking place in the photoprotective VAZ cycle pool (Violaxanthin, Antheraxanthin, Zeaxanthin) (*Figure 6*).

3.4 Light saturated photosynthesis rate and electron transport rate within the canopy of trees

Leaf gas exchange parameters and the electron transport rate of fully developed leaves were investigated at the study site in the first week of July, 2004 when experimental conditions did not indicate severe drought. Therefore these data can only be used as an indication of interspecific variation in photosynthetic parameters and description of photosynthetic efficiency of two oak species. Both species exhibited relatively low light saturated photosynthesis rate (Table 3) which changed with the light adaptation character of the leaves. *Q. petraea* exhibited two or three times higher $P_{\max}$ in sun leaves than in shade leaves. The decline of $P_{\max}$ within the canopy of *Q. cerris* was smaller. The transpiration rate of both species was also the highest in the upper part of the canopy but it showed slighter reduction towards the shade layer of trees (Table 3). Water use efficiency was higher for *Q. petraea* in each layer of the canopy. In contrast to low photosynthesis rate both species maintained relatively high light saturated ETR values. ETR was higher at saturation light intensity for both canopy layers of *Q. cerris* than for *Q. petraea* (Table 3).

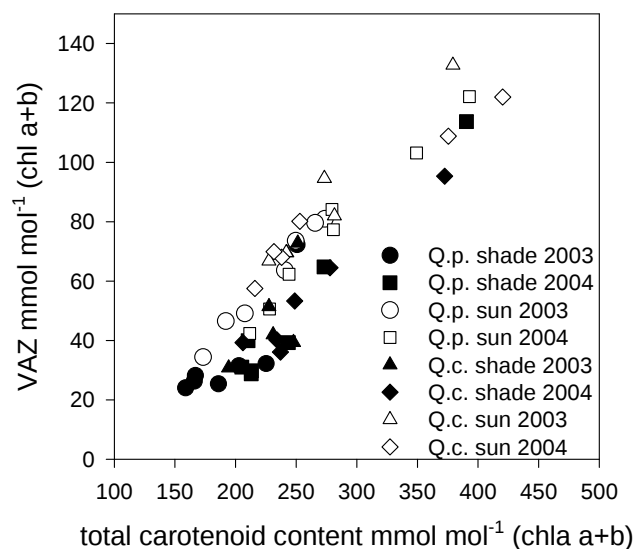


Figure 6. Changes in total carotenoid content and VAZ cycle pool in sun and shade leaves of *Q. petraea* and *Q. cerris* in spring and summer of 2003 and 2004.

Table 3. Stomatal conductance (g_s), light saturated CO_2 assimilation rate ($P_{\max}$), transpiration rate (E), Water use efficiency (WUE) and electron transport rate (ETR) of sun and shade leaves of *Quercus petraea* and *Quercus cerris*. The measurements were performed on 5-7 July 2004. Mean values and ± 1 SE are presented ($n = 18$).

		g_s ($mmol\ m^{-2}\ s^{-1}$)	$P_{\max}$ ($\mu mol\ m^{-2}\ s^{-1}$)	E ($mmol\ m^{-2}\ s^{-1}$)	WUE ($\mu mol\ CO_2\ mmol^{-1}\ H_2O$)	ETR ($\mu mol\ m^{-2}\ s^{-1}$)
<i>Q. petraea</i>	sun leaves	362.7 $\pm$ 26.7	8.33 $\pm$ 0.44	3.78 $\pm$ 0.13	1.82 $\pm$ 0.06	109.1 $\pm$ 18.4
	shade leaves	168.6 $\pm$ 11.9	3.34 $\pm$ 0.38	2.79 $\pm$ 0.09	1.08 $\pm$ 0.10	60.91 $\pm$ 11.5
<i>Q. Cerris</i>	sun leaves	486.9 $\pm$ 44.4	8.06 $\pm$ 0.54	3.73 $\pm$ 0.24	1.96 $\pm$ 0.11	126.7 $\pm$ 10.9
	shade leaves	349.6 $\pm$ 41.8	6.26 $\pm$ 0.56	3.29 $\pm$ 0.23	1.67 $\pm$ 0.09	109.4 $\pm$ 26.3

3.5 Seasonal changes of maximum photochemical efficiency of leaves

The seasonal course of maximal photochemical efficiency of PSII (Fv/Fm) measured at noon in the dark-adapted state (Figure 7) resembled that of chlorophylls (Figure 5) and leaf growth (Figure 4). In the early growing season leaves exhibited lower Fv/Fm values in each year. Fv/Fm was always lower in sun leaves of both oak species in each year but the variability of Fv/Fm within the tree canopy was higher in *Q. petraea*. In 2003 Fv/Fm ratios were slightly lower (by 1-3%) for fully expanded sun and shade leaves in both species.

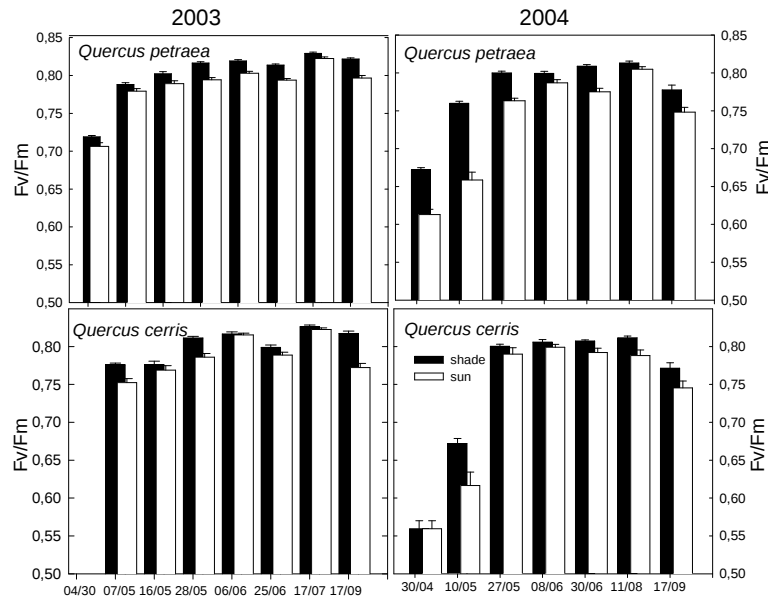


Figure 7. Seasonal changes in maximal photochemical efficiency measured at noon in sun and shade leaves of two oak species in 2003 and 2004.

4 DISCUSSION

The years in which the investigations were performed differed significantly in weather conditions. 2003 was an extreme year for the forest stand and trees experienced drought stress from the start of crown development. Growing season of 2004 was colder and rainfall during the main period of canopy expansion was significantly higher and showed more even distribution from April to September. In 2003 the soil moisture content decreased to around 15% in June and July. In May and June of 2003, during the main period of leaf development, the temperature was higher than in 2004.

Leaf growth of *Q. petraea* was less tolerant to drought than that of *Q. cerris*. Drought slightly affected the leaf area expansion of *Q. petraea* but reduced significantly the leaf mass increment. It suggests that sessile oak invested less assimilates into producing structural carbohydrates in the dry year (2003) than did *Q. cerris*, but instead it maintained a similar leaf area as in 2004. As a result, SLM was lower in 2003 than in 2004. In contrast to *Q. petraea*, *Q. cerris* showed small plasticity of leaf growth traits in corresponding canopy layers in response to the alteration of soil water availability in different years and maintained smaller leaf area and leaf mass but higher SLM, particularly in sun leaves.

In comparative studies with a wide range of trees species it was revealed that SLM is positive correlated with modulus of leaves' cell wall elasticity which inversely relates to cell wall elasticity (Salleo – Lo Gullo 1990). This relationship is a well accepted indicator of interspecific differences in drought tolerance. In general, tree species showing lower SLM and

lower modulus of elasticity (more elastic cell wall in leaf tissues) occur preferably in more mesic sites. However, species with higher SLM and less elastic leaf area are better adapted to drier sites (Corcuera et al. 2002). It can also be stated that the functional correlation between the two leaf traits is not so well revealed. It is assumed that SLM depends more on the amount of mechanical tissue (mainly cells with lignified cell wall) and thereby reflecting the leaf density and thickness, while modulus of elasticity is more sensitive to thickness and cellulose content of cell wall, indicating primarily the maximal amount of water accumulated in cells at full turgor of leaves.

The lower SLM and more elastic cell walls of leaves observed in *Q. petraea* in 2003 allow this species to store adequate amounts of water at low leaf (and soil) water potential such that it can afford to transpire more than was transported from the roots. In this way *Q. petraea* acclimated to the severe drought conditions through exhibiting a water-spending strategy. In comparison, the higher SLM of *Q. cerris* supposed less elastic cell walls and more rigid anatomy in the leaf that allowed the adoption of a water-saving strategy. The two different strategies for controlling the leaf water relations may be advantageous for the two species co-existing at the same site. The water-spending strategy of *Q. petraea* can permit it to absorb water from the soil at the expense of a larger loss of water through transpiration; therefore this species must adopt a specific drought tolerance mechanism for maintaining the leaf turgor for leaf physiology as optimal as possible when leaf water potential is reduced. However, such a strategy cannot be sufficient when drought persists. At the same period *Q. cerris* showed a water-saving strategy that allows it to avoid the larger water loss and moderate the water absorption. Therefore this species may be more successful in prolonged drought periods.

These different strategies might explain the differences in water use efficiency of leaves between the two species. *Q. cerris* was characterised by a higher water use efficiency during the same measurement conditions than *Q. petraea*.

The rate of leaf mass increase was very similar in the initial phase of leaf development in both study years but it was substantially reduced earlier in 2003 and continued more slowly until the date of full expansion of leaves than in 2004. Nevertheless, not only zero growth but reduction of average leaf mass was also observed due to the prolonged drought in June particularly for *Q. petraea*. As a result, we observed a transient phase of negative leaf growth rate reflecting the impairment of leaf carbon balance (Mészáros et al. 2007) which could only recover after the short heavy rain in July.

Alteration of growth traits during drought has been reported for other tree species. Sessile oak seedlings adapted to drought by reducing the leaf:root ratio (Thomas 2000) and decreasing the ratio of leaf to fine root biomass (Thomas – Gausling 2000). Large reductions in annual biomass and tree circumference for adult pine and beech trees were also reported as a result of drought in 2003 as compared to humid years (Granier et al. 2007).

The chlorophyll contents of shade and sun leaves were higher in 2003 than in 2004, particularly in *Q. petraea*. The higher leaf chlorophyll content per unit of dry matter in drier year can be considered as a compensating mechanism for the reduced leaf area and mass.

Studies on a wide range of species showed that maintenance of photosynthesis rate at the level which provides a positive carbon balance of leaves during stress requires efficient photoprotection of photosynthetic apparatus including carotenoids (Long et al. 1994) In contrast to *Q. petraea*, *Q. cerris* invested less in synthesis of carotenoids in the dry year than in the humid year which suggests that other leaf traits and processes may also be effective in avoiding the effects of excess light under limiting water availability.

Chlorophylls and carotenoids exhibited clear seasonal trends for both species. In spring carotenoids were synthesised earlier than chlorophylls and showed high concentrations in young leaves in the whole crown of the trees. It reflected the fact that these compounds

played important role in photoprotection of expanding tree crown before the photochemical efficiency and the carbon assimilation capacity of trees were low and chloroplast development was incomplete. Carotenoids/chlorophyll ratios correlated negatively with the Fv/Fm values during the growing seasons.

Depression of Fv/Fm in young leaves took place with a simultaneous adjustment of the pigment composition in both species. The high carotenoid content in developing leaves seems to be an important stabilising biochemical trait of the two species for the balance between light absorption and its utilisation in the photochemical reactions particularly when heat stress and water stress may result in more serious down-regulation of photosynthetic CO₂ assimilation such as appeared in the hot spring and early summer of 2003. The depressed Fv/Fm and down-regulated CO₂ assimilation in spring obviously increase the demands on photoprotective processes such as non-assimilatory electron transport and non-radiative dissipation of absorbed light energy (Demmig-Adams – Adams 1992). The non-radiative (heat) dissipation of excess light energy is mediated in leaves of oak species by the operation of xanthophyll cycles, a largest part of VAZ cycle and a small part of lutein-epoxid cycle (Mészáros et al. 2005). Young leaves of both species accumulated VAZ cycle pigments (violaxanthin, antheraxanthin, zeaxanthin) by 1,5-2,5 times higher than fully developed leaves. It suggests a greater demand on photoprotection against the high light intensity in developing leaves of the tree crown which may be accelerated significantly when other environmental stresses appear. The low midday values of Fv/Fm in spring indicated the susceptibility of photosynthetic apparatus of both species to photoinhibition.

Our measurements showed that both species exhibited relatively low $P_{\max}$ of fully developed sun leaves at saturated light which was also reported for other late-successional tree species (Bassow – Bazzaz 1998). However, in contrast to the low CO₂ assimilation rate, both oak species showed high ETRs at saturation light intensity. Due to a loose canopy structure *Q. cerris* maintains a relatively higher ETR not only in sun leaves but also in the shade leaves. These results suggest that sun exposed leaves of both species must develop substantial non-assimilatory (photorespiratory) electron utilisation for avoiding PSII photoinhibition (Kozaki – Takeba 1996) in the summer period when high light levels are accompanied by high temperatures. Increased photorespiration has also been reported to be involved in the maintenance of high ETR for a savanna tree species (Franco – Lüttge 2002) and for Norway spruce (Spunda et al. 2005).

Increased photorespiratory electron utilisation can also explain that in spite of relatively low $P_{\max}$ both species have the capacity to maintain high maximal photochemical efficiency of PSII (Fv/Fm) in summer. It also suggested that functioning of photosynthetic apparatus was generally less impacted even during summer drought than leaf growth, and could maintain a reduced but positive carbon balance of leaves, with the exception of a negative growth rate for *Q. petraea* in June 2003. The mean midday levels of Fv/Fm of fully developed leaves remained around 0.80 in both summer periods: *Q. cerris*: sun leaves 0.803 (2003), 0.792 (2004), shade leaves 0.813 (2003), 0.806 (2004); *Q. petraea*: sun leaves 0.801 (2003), 0.782 (2004), shade leaves 0.816 (2003), 0.805 (2004). This reflects a high degree of resistance of the photosynthetic apparatus to chronic photoinhibition in summer which was also reported for other tree species (Spunda et al. 2005, Mészáros et al. 1998). However, the midday levels of Fv/Fm were lower than the maximal value (0.832 ± 0.004) potentially reached by dark-adapted leaves of plants with optimal physiological condition (Björkmann – Demmig-Adams, 1987) in the absence of stress.

Beside the potential involvement of photorespiratory electron transport in photoprotection the low CO₂ assimilation rate also increases the demand on non-radiative dissipation of absorbed light energy in the upper part of crown in the summer period. However, in contrast

to fully expanded leaves the higher VAZ pool in spring indicated that the latter process might have a more significant role in photoprotection in young leaves of both species.

Our results show that sun leaves of both species were always characterised by more depressed Fv/Fm and larger VAZ cycle pool than shade leaves during the whole growing season of both years. The midday depression of Fv/Fm correlated with the de-epoxidation of violaxanthin into antheraxanthin and zeaxanthin, and the zeaxanthin dependent heat dissipation in sun leaves (Mészáros et al. 2006). Both species showed larger impairment of maximal photochemical efficiency and lower Fv/Fm in the wetter year (2004) than in 2003. This indicated lasting drought effects on the photochemical activity of leaves of both species, but *Q. petraea* was more affected than *Q. cerris*. Such a time lag of drought occurring during the previous growing season on the physiological traits was also reported for other species (Bréda et al. 2006, Granier et al 2007). This may be a consequence of reduced amount of carbohydrates, lipid and protein reserves formed in the end of 2003 and also the damage to roots and irreversible xylem embolism. These together might weaken the trees for long period and accelerate their susceptibility to stresses including the large scale gradation of phytophagous insects particularly at sites with low fertility and transitional position. However, the questions of how drought extremes may influence the competition between the two existing oak species, and whether they may result in serious tree dieback in the investigated forest, require further studies.

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