

Springtime Leaf Development of Mature Sessile Oak Trees as Based on Multi-Seasonal Monitoring Data

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Abstract – Based on a four year leaf growth data-set we modelled the thermal time-dependent leaf ontogeny in upper and lower canopy layers of mature sessile oak trees, in a *Quercetum petraeae-cerris* forest stand (NE Hungary). Our regression models revealed no considerable differences between the timing of leaf unfolding and leaf expansion of different canopy layers. On the other hand seasonal course in leaf mass-to-area ratio (LMA) indicated that sun leaves needed considerably longer thermal time to fully develop their anatomical structures compared to shade leaves. LMA of sun leaves was higher during the whole leaf maturation process suggesting that ‘sun’ and ‘shade’ characteristics develop in very early stage of leaf ontogeny. Functioning of photosynthetic apparatus (F_v/F_o) in shade leaves have built up faster and performed better in all developmental stages which could be attributed to two main factors: 1) very early determination of leaf traits as a function of light environment and 2) evolving shading effect of upper canopy layer eliminates photoinhibition in lower leaves.

leaf ontogeny / leaf traits / leaf morphology / chlorophyll fluorescence / light environment / *Quercus petraea*

Kivonat – Levélnövekedés és a fotokémiai hatékonyság tavaszi felépülése kocsánytalan tölgyfák lombkoronájában, többéves monitoring adatok alapján. Jelen munkánk során több levéljellemező változása alapján modelleztük a levélfejlődés folyamatait a hősszeg függvényében, egy mérsékelt övi cseres-tölgyes erdőállomány idős kocsánytalan tölgyfáinak alsó és felső lombkorona-rétegében. Az eredményeink alapján a levélterület kialakulása a lombkorona alsó és felső részében egyszerre kezdődik és fejeződik be. A fénylevelek esetében a levéltömeg/terület arány (LMA) később érte el a nyári értékét, és a levélfejlődés minden szakaszában nagyobb vastagságot és/vagy nagyobb sűrűséget jelzett, ami a fény- és árnyéklevél-tulajdonságok igen korai kialakulását jelzi. A levelekben a PSII kvantumhozam (F_v/F_o) szezonális fejlődését szintén befolyásolja a lombkorona-helyzet. Az árnyéklevelek a teljes fejlődési folyamat alatt magasabb F_v/F_o értékekkel rendelkeztek, és gyorsabban elérték a szezonális maximumukat, mint a fénylevelek. Az utóbbi eredmények szintén a fény- és árnyékjelleg korai determinációjára utalnak, továbbá jelzik azt is, hogy a levélterület-növekedéssel párhuzamosan kialakuló önárnyékolás sietteti a PSII kvantumhozam felépülését.

levélfejlődés / levéltulajdonságok / levélmorfológia / klorofill fluoreszcencia / fényklíma / *Quercus petraea*

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1 INTRODUCTION

Springtime evolution of morphological, anatomical and physiological leaf traits in deciduous communities has fundamental impact on ecosystem functioning (Nizinski – Saugier 1988, Bequet et al. 2011). Leaf area and photosynthetic efficiency as quantitative and qualitative aspects determine carbon assimilating potential of any given plant in the community (Muraoka et al. 2010). Expanding leaves of upper canopy layers affects the functioning of lower layers including certain parts of the plant's own canopy (Umeki et al. 2010, Bequet et al. 2011). In deciduous forests mature trees with multi-layered crown architecture are especially exposed to this shading effect (Valladares – Niinemets 2007, Mészáros et al. 2007, Szöllősi et al. 2010).

A possible strategy for minimizing the effects of self-shading is the proper spatial and temporal distribution of leaves as for instance herbaceous dicots form their foliage (Poorter et al. 2009). Plants applying this strategy of successive leaf phenology form their first leaves at the proximal end of their shoots and the leaf expansion proceeds successively to distal regions of the shoot system thus allowing the younger leaves to capture more light energy (Umeki et al. 2010.). Other plant species with nearly simultaneous leaf flushing, such as a number of broad-leaved temperate woody species (Poorter et al. 2009, Szöllősi et al. 2010), optimize their leaf traits in order to gain the best performance (Koike et al. 2001). A typical adaptive mechanism for maximal utilization of the available light energy along the vertical profile of the canopy is formation of sun and shade leaves, respectively (Jurik 1986, Givnish 1988, Yano – Terashima 2001, Terashima et al. 2005, Poorter et al. 2009). Sun leaves are adapted to intense, direct irradiation, higher temperature and higher water vapour deficit by evolving xeromorphic traits (Terashima et al. 2005, Mészáros et al. 2007, Poorter et al. 2009). Sun leaves have smaller and thicker leaf lamina, higher leaf mass-to-area ratio (LMA) due to thicker palisade parenchyma or/and larger density in the mesophyll, higher photosynthetic light compensation point and more powerful electron transport system (Yano – Terashima 2001).

Ontogeny of leaves is regulated dynamically in order to properly conform to a given microhabitat, involving e.g. duration of leaf cell division and expansion (Granier – Tardieu 2009). After leaf maturation, physical dimensions of leaves such as leaf area or leaf mass-to-area ratio are irreversibly determined in contrast to e.g. the photosynthetic pigment content, density and formation of chloroplasts (Poorter et al. 2009).

The present study deals with springtime development of leaf traits of mature sessile oak trees with special emphasis on the following questions:

- i) How does leaf maturation progress in the case of mature oak trees?
- ii) How do various leaf traits develop as a function of thermal time? Is there any difference between lower and upper canopy positions in this respect?
- iii) At what phase of leaf maturation do 'sun' and 'shade' characteristics in leaf traits appear?

For studying the above questions we used leaf morphological traits and chlorophyll fluorescence data obtained from multi-seasonal study of mature sessile oak trees (*Quercus petraea* [Matt.] Liebl.).

2 MATERIALS AND METHODS

2.1 Study site

Leaf development of mature sessile oak trees (*Quercus petraea* [Matt.] Liebl.) was monitored in the forest stand of Síkfőkút LTER Europe site (Bükk Mountains, NE Hungary; 47°90'N, 20°46'E, 320–340 m ASL). The site is covered by an approx. 100 years old coppice forest

predominantly consisting of sessile oak (*Quercus petraea*) and Turkey oak (*Quercus cerris*) in the canopy (*Quercetum petraeae-cerris*). The site was established for monitoring the forest structure and functions in 1972 (Jakucs 1985). Meteorological records are collected by a station set up on a 25 m high tower within the forest since 1973. The 30-year average (1973–2002) of annual mean of air temperature and total rainfall was 10.2 °C and 560.5 mm, respectively (Table 1). The growing season usually lasts from mid-April to mid-October at the site (Jakucs 1985, Szöllösi et al. 2010).

2.2 Meteorological background

In years of this study weather data were recorded automatically in every 30 min on the top of meteorological tower erected above the canopy of forest. Temperature and relative humidity were measured with Hobo ProSeries RH&Temp sensors, rainfall was measured with an automatic rain gauge connected to Hobo Micro Station (both produced by Onset Computer Corporation, Pocasset, USA).

2.3 Sampling and measurement

Leaf development was studied in four consequent growth seasons from 2006 to 2009. First leaf samplings were timed shortly after bud-break (mid-April) and were repeated weekly during springtime and later in every second or third week until fully matured state of leaves (late July). Four healthy, approx. 100 years old sessile oak trees were selected for the study (height: 17–20 m, DBH: 28–36 cm) growing close enough to the meteorological tower for easy canopy access.

Leaf samples were harvested on sunny days, between 11:00 a.m. and 15:00 p.m. from the upper (20 m, ‘sun leaves’) and lower (10 m ‘shade leaves’) canopy positions of each tree. As a result 10–20 leaves represented each canopy position of each tree.

2.3.1 Measured parameter

Chlorophyll fluorescence: *in vivo* chlorophyll fluorescence measurements were made using PAM-2000 fluorometer (Heinz Walz GmbH, Effeltrich, Germany). Harvested leaves were previously dark-adapted for 30 min in order to fully relax PSII reaction centers and thus gain maximal photochemical efficiency of samples. Minimal (F_o) and maximal fluorescence yields (F_m) of samples were measured in the middle region of adaxial leaf surfaces avoiding major leaf veins. Variable fluorescence was calculated as $F_v = F_m - F_o$ and was used to characterize the potential quantum yield of PSII photochemistry as the ratio of F_v/F_o (Babani – Lichtenthaler 1996, Lichtenthaler et al. 2005).

Leaf area (LA): a commercial digital scanner was used for leaf area measurements. Scanned images (300 dpi resolution) of leaves were processed with ImageJ image analysis software (Abramoff et al. 2004).

Leaf dry mass (LM): leaves were measured with analytical balance (± 0.0001 g accuracy) after drying at 85 °C till constant weight. Based on LA and LM data leaf mass area ($LMA = LM/LA$, g dm⁻²) of each leaf was calculated.

2.4 Data processing

Weather data: as the process of leaf phenology and ontogeny is strongly temperature-dependent (Nizinski – Saugier 1988, Bequet et al. 2011) thermal time – expressed in °C days – was used to describe chronology in development of leaf traits instead of day of year (DOY) basis. Thermal age of leaves was calculated as cumulative daily mean air temperature summed from DOY 100 (10th April) of each year, the date around the leaf unfolding usually begins.

Leaf parameters: respective data of sample trees were collected and merged on sampling date and canopy position basis (20–40 samples per sampling date and canopy position). Medians of leaf traits were used for describing sun and shade canopy layers at a given sampling date. The four-year leaf growth monitoring data base allowed us to utilize 28–28 leaf morphological (LA and LMA) and 27–27 chlorophyll fluorescence (F_v/F_o) data points as a total for sun and shade leaves, respectively.

Modeling of leaf maturation: merged leaf trait data series from all sampling years were analyzed as a function of thermal time using non-linear regression function of Sigmaplot 10 (Systat Software, Inc.) in order to mathematically describe leaf expansion. Leaves were considered fully mature from the aspect of a given leaf trait after reaching 95% of their summer value (Cookson et al. 2007) calculated by the regression model. After defining the characteristic phases of leaf maturation, the comparable medians of sun and shade data within a given phase were analyzed by paired Wilcoxon test function of PAST 2.16 (Hammer et al. 2001). Differences were considered to be significant at two-tailed $p < 0.05$ level.

3 RESULTS

The annual mean air temperature was higher during the study years as compared to the average of base period from 1973 to 2002 (*Table 1*). In each year the annual mean temperature was above 11.0 °C, and in 2007 it exceeded 12.0 °C. Total rainfall was slightly lower than the 30-year average. Among the study years 2007 was the warmest and driest and 2006 was the most humid in the main period of leaf growth (10th April – 31st July) (*Table 1*).

Table 1. The annual mean air temperature and total rainfall at Síkfökút LTER forest site during the study years (2006–2009) compared to the period (1973–2002) and the mean temperature and rainfall in the period of leaf growth (10th April – 31st July)

		2006	2007	2008	2009	Average 1973–2002	Average 2006–2009
Mean air temperature (°C)	Yearly	11.3	12.2	11.4	11.3	10.2	11.6
	Leaf growth period DOY 100–212	18.4	19.8	18.1	18.5	–	18.7
Total rainfall (mm)	Yearly	588	552	499	554	561	548
	Leaf growth period DOY 100–212	332	168	246	203	–	237

3.1 Expansion of leaf area

Seasonal development of leaf area showed sigmoid-shape trend with the thermal time (*Figure 1*), that was described by the following function:

$$LA_x = a / (1 + e^{-(x-x_0)/b}) \quad (1)$$

Where:

LA_x is the leaf area at a given thermal time x ,

x_0 is the inflection point of the curve (the point of the maximal LA-growth rate),

a is the summer (maximal) LA,

b is the coefficient of inclination.

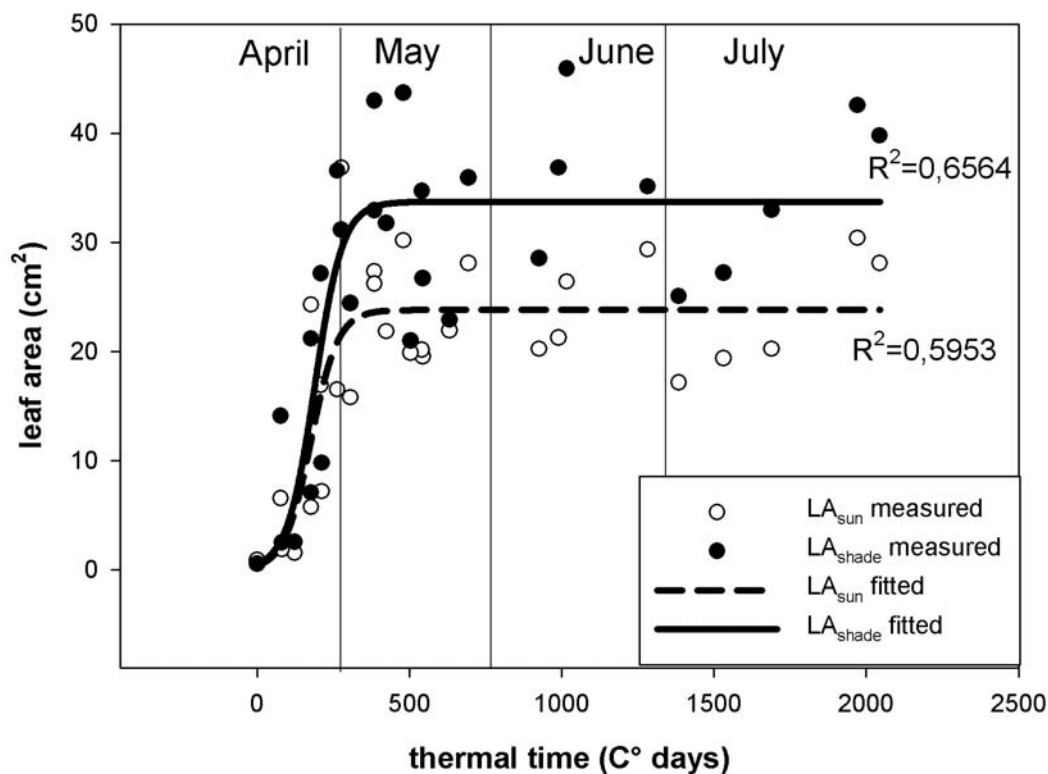


Figure 1. Temporal course of leaf area (LA) expansion of mature sessile oak trees. Each open and closed circle represents the median of 20–40 leaves collected from the upper (sun) or lower (shade) canopy position of 4 mature sessile oak trees, respectively, at each sampling date characterized by thermal time. Dashed and solid trendlines are calculated seasonal courses of LA in the upper and lower canopy positions, respectively. Vertical lines indicate the average thermal time for the first day of months in the study period 2006–2009.

LA development began with a short phase of slower increase ('lag-phase'). After that leaf area expanded rapidly and almost linearly as a function of cumulative temperature until reaching its summer value (Cookson et al. 2007, Bequet et al. 2011) (Figure 1). Calculated LA of sun and shade leaves at the start (0 °C days) were similar, that is 0.4 and 0.5 cm², respectively. Sun and shade leaves reached the summer state of LA nearly at the same thermal age (305 and 323 °C days for sun and shade leaves, respectively). Shade leaves had significantly ($p < 0.001$, $n = 18$) higher summer LA (33.7 cm²) than sun leaves (23.8 cm²), similarly to other reported data on woody species (see e.g.: Koike et al. 2001, Poorter et al. 2009). Assuming that the two types of leaves become mature simultaneously, different rates of leaf expansion could be expected for the two canopy positions (Figure 1). Based on regression models, the maximal rates of leaf expansion were 0.136 and 0.185 cm² cm⁻² °C days⁻¹ for sun and shade leaves, respectively. However, the pairwise comparison of medians did not indicate significant difference ($p = 0.105$, $n = 10$).

3.2 Seasonal building up of leaf structure

Building up of leaf mass-to-area ratio (LMA) exhibits a seasonal course with three phases (Figure 2) (Jurik 1986) and could be described by a peak function:

$$LMA_x = LMA_s + a / (1 + ((x - x_0) / b)^2) \quad (2)$$

Where:

- LMA_x is the specific leaf mass area at a given thermal time x ,
 x_0 is the thermal time at the point of seasonal minimum,
 LMA_s is the summer (maximal) LMA,
 a is the constant for the 'amplitude' i.e. seasonal minimal LMA,
 b is the constant of curvature.

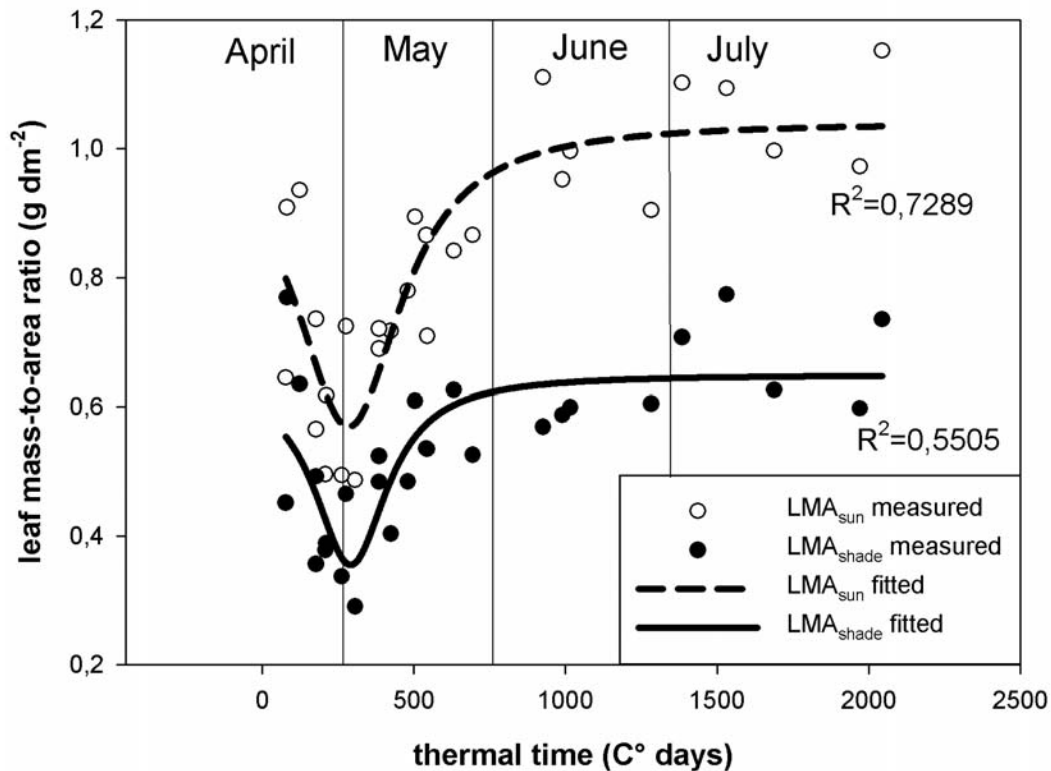


Figure 2. Temporal course of leaf mass-to-area ratio (LMA) of mature sessile oak trees. Each open and closed circle represents the median of 20–40 leaves collected from the upper (sun) or lower (shade) canopy position of 4 mature sessile oak trees, respectively, at each sampling date characterized by thermal time. Dashed and solid trendlines are calculated seasonal courses of LMA in the upper and lower canopy positions, respectively. Vertical lines indicate the average thermal time for the first day of months in the study period 2006–2009.

At the start (0 °C days) both sun and shade leaves exhibited relatively high LMA values (0.872 and 0.589 g dm⁻² for sun and shade leaves, respectively). During leaf expansion LMA fell rapidly till its seasonal minimum in both canopy positions (0.569 and 0.355 g dm⁻² for sun and shade leaves, respectively) at approximately the same thermal age (284 and 291 °C days for sun and shade leaves, respectively) (Figure 2). After that point, LMA increased first rapidly and then moderately until leaves reached their mature state at 864 °C days (sun leaves, LMA = 1.037 g dm⁻²) and 702 °C days (shade leaves, LMA = 0.648 g dm⁻²), respectively (Figure 2). The regression models show that LMA of sun leaves was higher in all three developmental stages (0–291 °C days; 291–864 °C days; > 864 °C days) than that of shade leaves, and the pairwise comparisons of LMA medians confirmed these differences (for the three phases $p = 0.004$, $n = 9$; $p = 0.002$, $n = 10$ and $p = 0.004$, $n = 9$, respectively).

3.3 Building up of PSII potential quantum yield

Potential quantum yield of PSII photochemistry (F_v/F_o) changed during the leaf maturation process and showed a saturating pattern (Babani – Lichtenthaler 1996, Szöllösi et al. 2010) (Figure 1) characterized by eq. (3):

$$F_v/F_{o,x} = F_v/F_{o,0} + a \cdot (1 - e^{(-b \cdot x)}) \quad (3)$$

Where:

- $F_v/F_{o,x}$ is the potential photochemical quantum yield at a given thermal time x ,
 $F_v/F_{o,0}$ is F_v/F_o at thermal time 0 °C day (start),
 $F_v/F_{o,0} + a$ is the summer (maximal) F_v/F_o ,
 b is the coefficient of saturation (curvature).

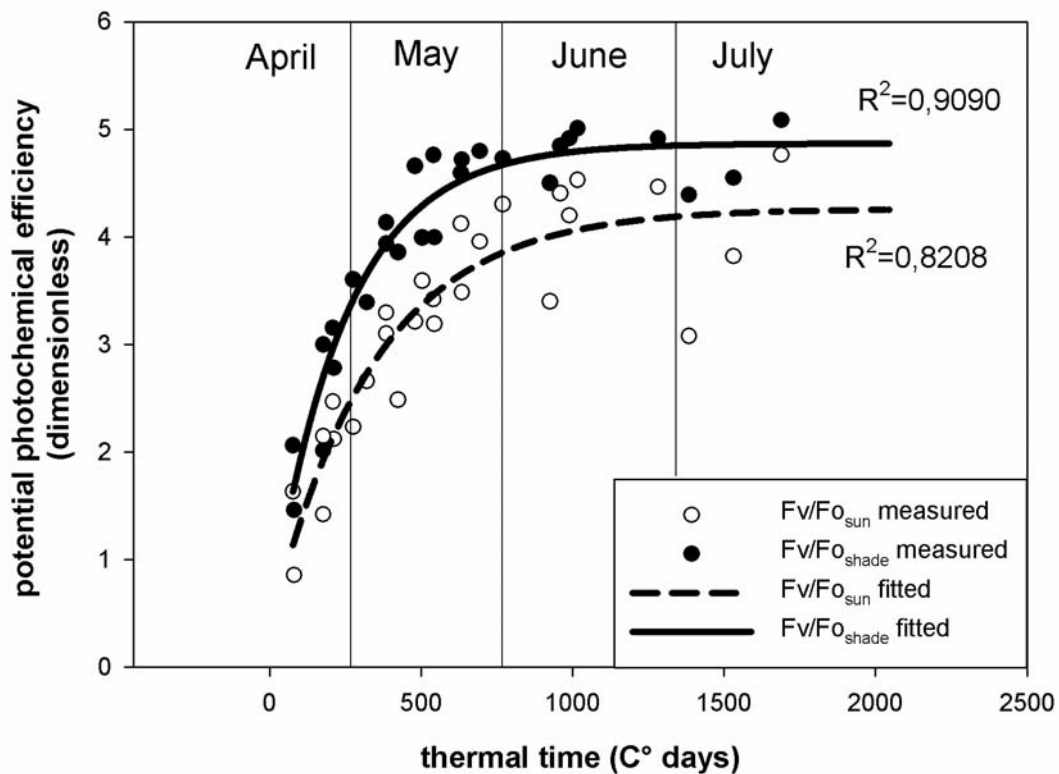


Figure 3. Temporal course of potential quantum yield of PSII photochemistry (F_v/F_o). Each open and closed circle represents median of 20–40 leaves collected from the upper (sun) or lower (shade) canopy position of 4 mature sessile oak trees, respectively, at each sampling date characterized as thermal time. Dashed and solid trendlines are calculated seasonal courses of F_v/F_o in the upper and lower canopy positions, respectively. Vertical lines indicate the average thermal time for the first day of months in the study period 2006–2009.

F_v/F_o of both sun and shade leaves showed continuous increase after leaf unfolding until reaching their mature state (Figure 3). The regression line fitted to F_v/F_o values of shade leaves is running slightly higher than that of sun leaves. At 0 °C days F_v/F_o was 0.45 in shade leaves and 0.34 in sun leaves. The fitted regression curve reflected significantly ($p < 0.001$; $n = 20$) faster development of F_v/F_o in shade leaves ($0.018 \text{ °C days}^{-1}$ as a maximum) that reached their summer maximum after 724 °C days. F_v/F_o of sun leaves saturated slower

(0.011 °C days⁻¹ as a maximum) and required 950 °C days to reach the maximal value. The difference in potential photochemical performances between the two canopy positions did not disappear. F_v/F_o was significantly ($p = 0.015$; $n = 7$) higher in shade leaves (4.867) than in sun leaves (4.261) (Figure 3).

4 DISCUSSION

Proper timing of leaf unfolding and maturation is essential for deciduous forest trees in order to avoid unfavourable periods and utilize efficiently favourable ones. Leaf phenology of canopy trees and physiological changes during leaf maturation basically determine the functioning of the whole forest ecosystem through their actual carbon balance and – as an additional effect – by shading lower canopy layers.

Based on four-year leaf growth monitoring data set we analysed the leaf maturation process in the upper and lower canopy layers of mature sessile oak trees in a North-east Hungarian forest stand.

As the underlying processes in leaf phenology are strongly temperature-dependent (Nizinski – Saugier 1988, Bequet et al. 2011) we applied thermal age of leaves as the independent variable in our models instead of days of the year. Our models revealed no considerable differences in the timing of leaf unfolding and leaf expansion between the two different canopy layers. LA values at the starting point of our regression models (0 °C day) confirm that both types of leaves unfold at the same time (Poorter et al. 2009, Szöllősi et al. 2010), shortly before DOY 100 (the starting day used in our analysis). From that point leaves required only 3 weeks (approx. 300 °C days) for reaching their fully expanded state, irrespective of their canopy position and of their summer mature LA. Leaves in the lower part of tree crown usually have larger LA than in the upper layers (Koike et al. 2001, Poorter et al. 2009). Our results indicated the similar vertical pattern of LA for sessile oak with 42% higher value for shade leaves. Shade leaves expanded faster than sun leaves and required similar time interval to reach their final LA.

Seasonal course in leaf mass-to-area ratio – which trait mainly refers to the anatomy of leaf mesophyll (Terashima et al. 2005, Poorter et al. 2009) – was different from that of LA (Jurik 1986). As leaf expansion began, LMA dropped sharply indicating the allocation of organic compounds for enlargement of leaf blades and reached its seasonal minimum at around 290 °C days, shortly before the end of leaf expansion (Jurik 1986, Poorter et al. 2009). Sun leaves of sessile oak trees exhibited higher LMA that was comparable with those of other species (Givnish 1988, Koike et al. 2001, Aranda et al. 2004). LMA of sun leaves was higher during the whole leaf maturation process which suggests that ‘sun’ and ‘shade’ characteristics develop in the very early stage of leaf maturation (Eschrich et al. 1989, Yano – Terashima 2001, Terashima et al. 2005). The thickening process of leaf blade was different in leaves from upper and lower canopy positions. The former ones required considerably longer thermal time for the full development of anatomical structures than the latter ones.

Characteristics of leaf development in dicotyledonous plants differ from that of monocotyledonous species (Croxdale and Omasa 1990, Granier – Tardieu 2009). In contrast to monocotyledonous species where assimilating tissues reach their mature state right after leaving the growing zone of leaf, the dicotyledonous leaves undergo gradual maturation, which is not uniform across the whole leaf blade but progresses from the leaf tip to the leaf basis. This maturation process is reflected by the seasonal course of potential quantum yield of PSII photochemistry (F_v/F_o) which shows a saturating pattern (Babani – Lichtenthaler 1996). Similar to LMA, photosynthetic apparatus of shade leaves matured faster and performed better in all developmental periods as compared to sun leaves. This difference

could be attributed to two factors: 1) very early determination of leaf traits as a function of light environment (Yano – Terashima 2001), which results in anatomical specialization (Eschrich et al. 1989) allowing a faster building up of summer F_v/F_o in shade leaves, and 2) the chronic photoinhibition of sun leaves (Babani – Lichtenthaler 1996, Lichtenthaler et al. 2005). At the beginning of leaf development, both the structure of photosynthetic apparatus and defence mechanisms against excess light are far from their maximal efficiency resulting in considerable photoinhibition of photosystems (Croxdale – Omasa 1990, Szöllősi et al. 2010). When the tree canopy is approaching its summer state – from the aspect of LA and LMA – photoinhibition gradually decreases in leaves of lower canopy layers as a result of shading effect by upper layers. Sun leaves as an opposite have to cope with photoinhibition during their entire lifespan which results in lower (Lichtenthaler et al. 2005) and slower development of F_v/F_o due to the significant investment into defence against excess light.

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