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Research Article

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Daily dynamics of photosynthetic parameters in beech population under periodical drought conditions

Abstract: The paper presents the impact of periodic soil drought on physiological parameters important for bioproductivity of mountain beech populations. The investigated forest population was located near Fruška gora mountain peak, where water runs off quickly, and consequently lack of soil humidity develops very often. Decreasing trends of photosynthesis, transpiration, water use efficiency and stomatal conductance (gs) during the growing season were evident, in correlation with a shortage of precipitation. Diurnally, photosynthesis of beech leaves showed rhythmical changes. It was the most intensive in the morning, then decreased between noon and 1 pm, and increased again during early afternoon. High leaf temperature and water deficit in the deeper soil layers caused a decreasing trend in photosynthesis and daily rhythmic changes of the transpiration rate and water use efficiency. Although surface soil water capacity did not show a significant decreasing trend from July to September, a lack of precipitation was observed, which probably caused a lack of moisture in deeper soil layers, resulting in a decline in photosynthesis and transpiration. Physiological status, linked to primary photosynthetic productivity of forests, could be a significant indicator of environmental conditions and trends in climate changes.

Keywords: beech forest, drought impact, climate change, mountain population

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1 Introduction

Monitoring of mountain forest ecosystems in specific humidity and temperature conditions is of high importance, because forests are noted as important terrestrial carbon sinks that partially compensate for global increases of atmospheric CO_2. Some forest studies predicted that the increase of CO_2 assimilation by forests will be especially significant in the first half of the 21st century [1,2]. Most predictions of climate change suggest that some site-specific water and temperature stress will occur more frequently in the future [3]. Photosynthesis is a main process which determines life on Earth, through the production of O_2 and organic compounds, but on the other hand, it plays an important role in the decrease of atmospheric CO_2. Photosynthetic dynamics of plant populations are under substantial influence of ecological conditions.

Global rise in temperature can act as a stimulator of photosynthetic processes and determine a shift of forest species toward higher mountain altitudes [4-6]. High temperature is often followed by drought, and it has been observed that this factor could significantly reduce plant acclimation to higher temperatures or increased CO_2 levels during growing season [7-8].

Environmental stresses like high air temperature, high irradiance and high air vapor pressure cause strong midday depression of photosynthesis [9]. Besides high light intensity, other environmental non-optimal conditions, like temperature, water availability and CO_2 supply can cause photoinhibition which can be transitional, reflecting photosynthetic regulatory responses to excess absorbed light. High photosynthetic activity in unfavorable environmental conditions is a result of good stomatal conductance for gas exchange

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and good functioning of the photosystem II [10]. In mountain ecosystems of Central and Southern Europe, forest populations of beech (*Fagus sylvatica* L.) occupy an important position in biodiversity, and ecological stability of mountain areas, and they are biomass resources in the forest industry.

Beech species are sensitive to water deficiency in soil and respond to drought stress by a reduction in leaf water potentials as well as decreased leaf stomatal gas conductance and photosynthesis, all resulting in growth reduction [11,12]. Periodic soil water shortages together with air drought could reduce the growth and vitality of sensitive tree species, such as beech [13] .

In the Balkan region, an extensive drought and warm period was observed in summer 2012 (July, August and September). The aim of this paper was to determine the impact of this period of soil drought on physiological parameters important for bioproductivity of beech mountain populations. We investigated leaf net photosynthetic assimilation, the number and characteristics of stomata and stomatal conductance, photosynthetic pigment contents, rate of transpiration and WUE in beech populations located on Fruška gora mountain region in Republic of Serbia.

Results of physiological monitoring support scientifically based prediction of sustainable development of mountain forest ecosystems in correlation with actual climate changes.

2 Experimental procedures

The experimental site was located in Fruška gora National Park (Northern Serbia, altitude 538 m), a mountainous area surrounded by lowlands of the of Panonian plain (Fig. 1). The local altitude is 473 meters, and in the proximity of a dominant mountain ridge stretching over 25 km in the east-west direction, ranging in height from 400 up to 538 meters of altitude. The analyzed forest is mixed sessile oak–beech found in lessivated acid brown soil with an east-northeast exposure. The age of investigated trees was approximately 85 years old with diameter at breast height varying from 36 to 52 cm. Tree height varied from 23-29 m, with large crowns up to 2/3 of tree heights and crown canopy closure of stand about 0,7.

All measurements were conducted three times during the growing period in 2012. First measurement was taken July 18th, the second 12th August and the 3rd September 27th.

Rates of photosynthesis (P) and transpiration (T), along with stomatal conductance (gs), were measured using LC pro+ Portable Photosynthesis System, manufactured by ADC BioScientific Ltd. A temperature sensor in the leaf chamber of the device was used to measure temperature of leaves in ºC (Tl). Measurements were made every hour per day, with 12 replicates taken each hour. Water use efficiency (WUE) was calculated as the ratio between photosynthetic and transpiration rates (P/T). Light conditions for photosynthesis were set using the LCpro+ light unit, which emitted photosynthetically active radiation (PAR) at 1000 µmol m^{-2} s^{-1}. The air supply unit provided a flow of ambient air to the leaf chamber at a constant rate of 100 µmol s^{-1}. Temperature, humidity and CO_2 concentration were at ambient levels. Measurements were performed on four different beech trees, on leaves growing at two heights, in three replications.

Chlorophylls and carotenoids were extracted using 80% acetone. Absorbances at wavelengths 663

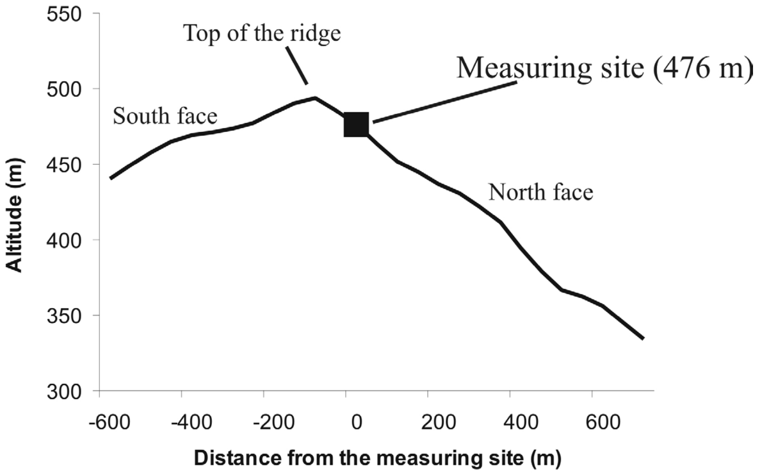

Figure 1: Altitude profile of Fruška gora and locality position of investigated beech population (■ – locality position at the mountain profile)

nm (chlorophyll a), 646 (chlorophyll b) and 470 nm (carotenoids) were measured by spectrophotometer and concentrations of pigments were calculated using molar absorption coefficients following equations determined by Lichtenthaler and Wellburn [14].

Pigment concentrations were calculated using 9 replicates and expressed as mg·g $^{-1}$ of dry plant weight. All analyses were conducted on leaves at lower branches, 1-1.5 meters from the soil surface.

Soil water capacity (SWC in %) was determined by examining soil samples taken from areas next to the measured tree, from the depth of 30 cm. Samples were weighed , dried at 60°C and weighed again. Finally, the soil was watered to maximum holding capacity, and measured. Our measurements were conducted on the basis of the following formula SWC = 100*(Sn-Sd)/Swm-Sd (Sn-weight of sampled soil, Sd-weight of dried soil, Swm-weight of soil which had been irrigated with maximum values of water).

Stomata prints were collected from the abaxial side of the beech leaf in the center leaf area on both sides of the main leaf vascular bundle. Total area of sampled stomata prints covered approximately 30% of each leaf. Every month 15 sample prints were collected from the leaves with the adhesive tape. Stomata were examined on each of the samples on five randomly chosen places, using microscope magnification of 40, so that the area of the field of view was 0.086 mm^2. These 75 measurements were conducted monthly, and the number of the stomata per mm^2 was defined on the basis of these measurements. The width and the length of the stomata were determined on the basis of 150 monthly measurements with 40 x magnification, using Motic Image 2000 program.

Precipitation and temperature data were obtained by the Republic Hydrometeorological Service of Serbia from the meteorological stations closest to the measuring localities. Precipitation was calculated as a total sum of rainfall during eight weeks before each measurement. Temperature was calculated as a daily average, using data collected during the four week period before each measurement.

All data were analyzed statistically using Duncan's multiple range test at the level of significance $p < 0.05$. The average values shown in table columns followed by the same letter did not differ significantly. Linear correlations (r) were calculated between measured parameters using average values.

3 Results

3.1 Photosynthesis

In July and August the photosynthetic rates achieved maximum values in the morning hours, between 8 am and 9 am. The second diurnal maximum of photosynthesis was in the afternoon, at 2 pm (Fig. 2a). Both daily increases of photosynthesis were statistically significant. In September, peak photosynthetic activity was found in the morning between 8 and 10 o'clock, but there was no significant increase of this parameter measured in the afternoon. If we compared the average photosynthetic activity in different months, it would be concluded that the highest value was found in July. A significant decrease in photosynthesis was recorded during the period from July to September.

3.2 Transpiration

Maximum transpiration rates were observed three times a day in July, between 8 and 10 am, then at 2 pm and at 6 pm (Fig. 2b). In August, a broad maximum was observed between 9 and 12 pm, then at 2 pm, whereas the afternoon maximum was absent. In September we recorded two periods of maximal transpiration rate: between 8 and 11 am and at 1 pm. These maximum rates of transpiration were significantly lower in Sepetember compared to values obtained in July and August.

3.3 Water Use Efficiency

WUE calculated as the ratio between photosynthetic and transpiration rates (P/T), showed similar diurnal dynamics as photosynthesis (Fig. 2c). It achieved its maximum in the morning at about 9 o'clock, and in the early afternoon at 2 pm in July and August. Maximum WUE observed in September was at 9 am and between noon and 1pm. Comparing monthly averages of WUE it could be concluded that there were significant decreases in this parameter during the investigated vegetation period from July to September.

3.4 Photosynthetic pigments, stomata and stomata conductance

There were no statistically significant changes observed in the content of photosynthetic pigments in different months (Fig. 3). Also, there were no significant changes observed in the width and length of stomata of the leaves

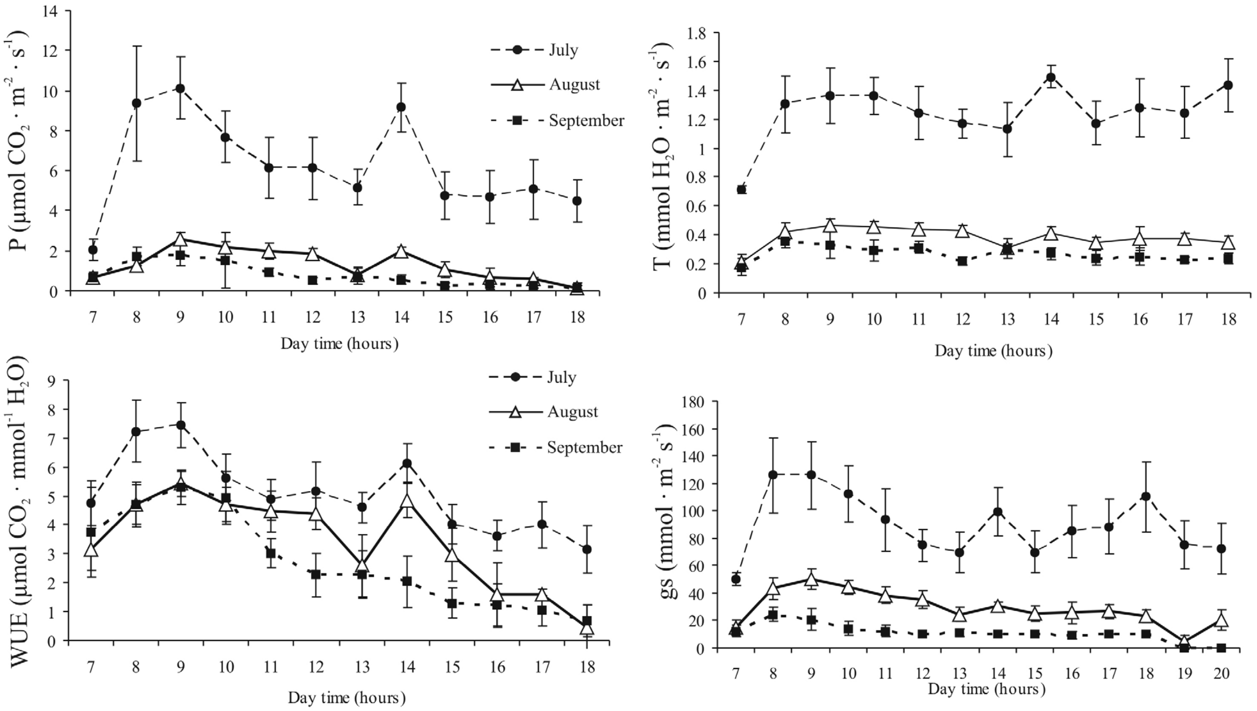

Figure 2: Measurement results made on beech leaves: P - net photosynthetic rate (μmolCO$_2$ m^{-2} s^{-1}), T - transpiration rate (mmolH$_2$O m^{-2} s^{-1}), WUE- water use efficiency (μmol CO$_2$ × mmol^{-1} H$_2$O), gs- stomatal conductance (mmol m^{-2}s^{-1})

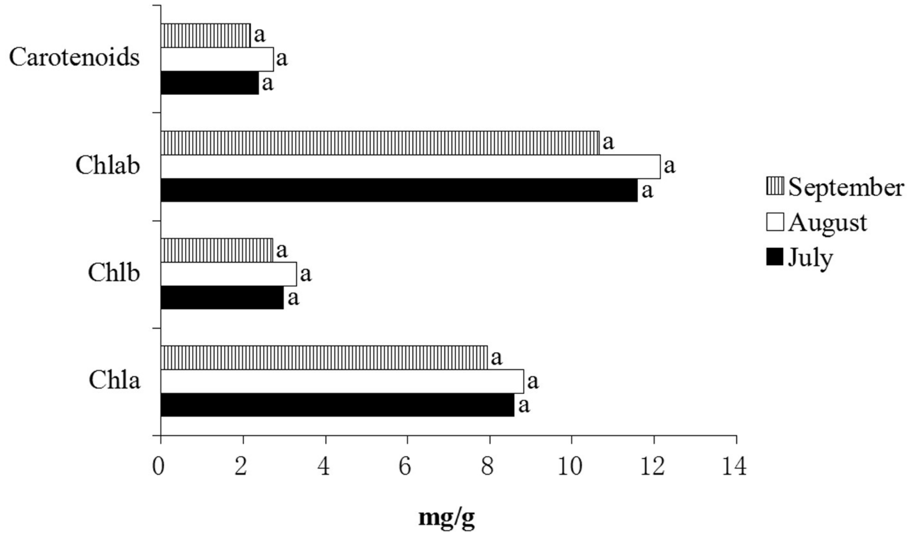

Figure 3: Content of photosynthetic pigments Chl *a*, Chl *b*, Chl *a+b* and carotenoids in beech leaves (mg·g $^{-1}$ dry matter)

during investigated vegetation period. Stomata number per mm^2 in September was significantly higher than July or August (Table 1). The rate of gs showed similar daily dynamics to photosynthesis, transpiration, and WUE (Fig. 2d). It achieved its maximum values three times a day: in the morning between 8 and 9 o'clock, then in the afternoon at 2 and at 6 pm.

3.5 The weather conditions during investigated period

By analyzing the data obtained, it could be concluded that eight weeks before the measurements (data obtained from May to September) there were no significant amounts of precipitation, and the weather

Table 1. Monthly changes in the width (μm), length (μm) and number of stomata

	Width	Length	Stomata number mm^{-2}
July	20.78 a	24.4 a	88.9 b
August	21.26 a	24.73 a	83.3 b
September	20.83 a	25.59 a	139.3 a

*Average values in each column followed with the same letter are not different for $p < 0.05$

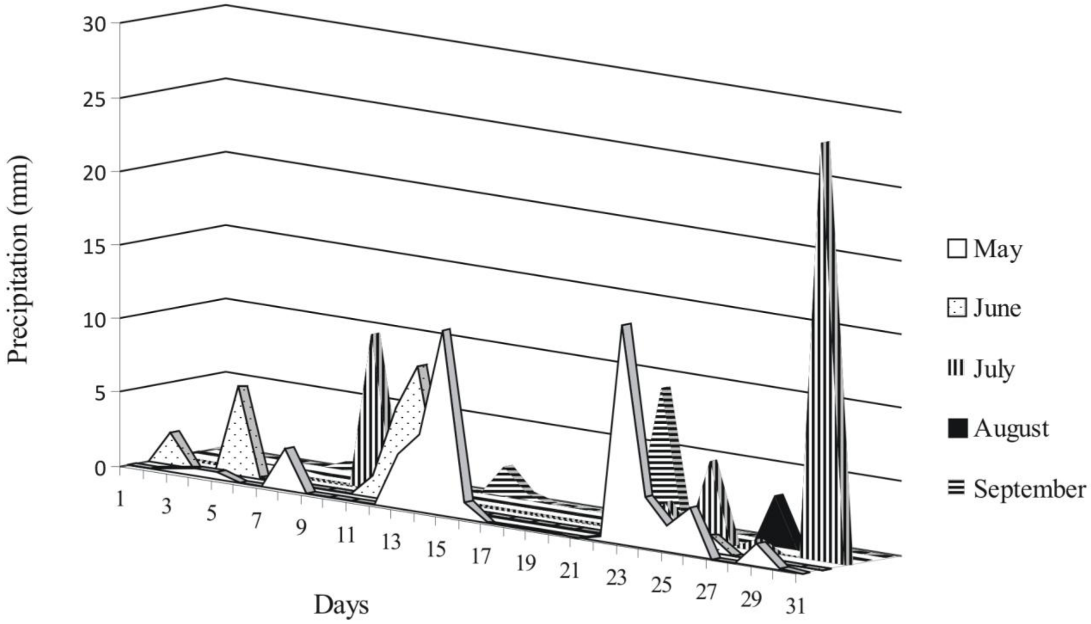

Figure 4: Monthly distribution of precipitation (data by Republic Hydro meteorological Service of Serbia)

was dry and warm (Fig. 4). Extremely low average precipitation was recorded in August (3.5 mm) and September (13.1 mm). The precipitation in other periods of vegetation was also low, but a little higher: May (52.2 mm), June (27.5 mm) and July (47.7 mm). During the summer of 2012, a shortage of precipitation was observed, and there was no significant difference in precipitation between months investigated.

Average temperature measured for four weeks before all three measurements were high, and the warmest period was before first measurement in July (26.11°C) (Fig. 5).

3.6 Soil water capacity

The soil water capacity measured for the soil surface (in the top of 30 cm) did not differ according to the period investigated from July to September (Table 2). Recorded values were very low, sub- optimal, indicating drought conditions.

Table 2. Monthly surface soil water capacity changes

	Soil water capacity
July	13.27 a
August	15.28 a
September	20.51 a

*Average values in each column followed with the same letter are not different for $p < 0.05$

3.7 Correlation

Correlations between daily averages of examined parameters were also done. Generally, photosynthesis, transpiration, WUE and stomatal conductance showed significant positive correlation with each other in all investigated periods (Table 3). Negative correlations were observed between leaf temperatures (Tl) and other investigated parameters (P, WUE and gs). The negative correlation between Tl and P was not significant in July,

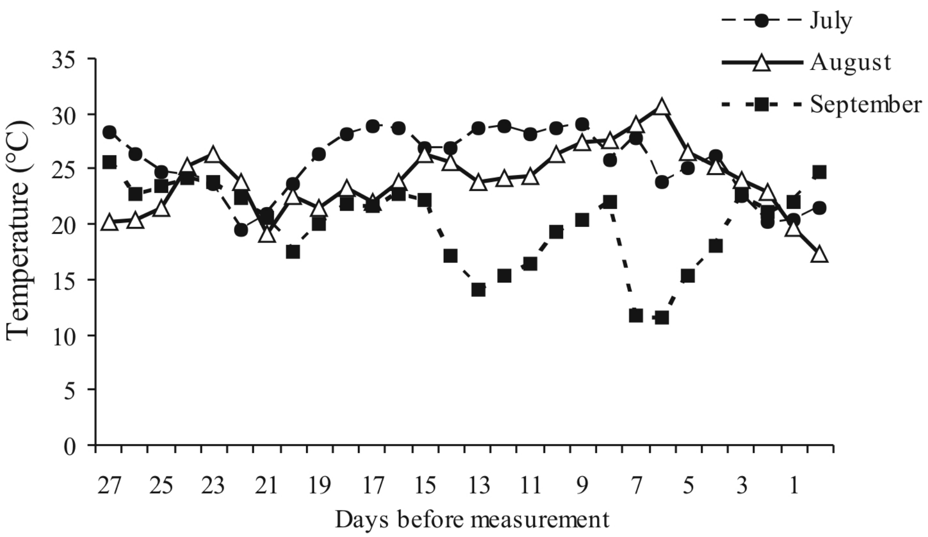

Figure 5: Average daily temperatures during four week period before each measurement (data by Republic Hydrometeorological Service of Serbia)

Table 3. Correlation between daily averages of investigated parameters (*p < 0.05)

		P	T	WUE	Tl	gs
July	P	1.00	0.69*	0.95*	-0.07	0.76*
	T	0.69*	1.00	0.46	0.23	0.84*
	WUE	0.95*	0.46	1.00	-0.14	0.59*
	Tl	-0.07	0.23	-0.14	1.00	-0.32
	gs	0.76*	0.84*	0.59*	-0.32	1.00
August	P	1.00	0.80*	0.97*	-0.58*	0.90*
	T	0.80*	1.00	0.64*	-0.29	0.85*
	WUE	0.97*	0.64*	1.00	-0.62*	0.82*
	Tl	-0.58*	-0.29	-0.62*	1.00	-0.53
	gs	0.90*	0.85*	0.82*	-0.53	1.00
September	P	1.00	0.74*	0.95*	-0.67*	0.91*
	T	0.74*	1.00	0.50	-0.19	0.69*
	WUE	0.95*	0.50	1.00	-0.76*	0.82*
	Tl	-0.67*	-0.19	-0.76*	1.00	-0.76*
		0.91*	0.69*	0.82*	-0.76*	1.00

but in August and September it was significant. The same was recorded for correlation between Tl and WUE, which was significant in August and September. In September a significant negative correlation was observed between Tl and gs, as well, probably because of the extensive shortage of precipitation.

If we compared the monthly averages of each investigated parameter, it was found that there was a positive and significant correlation between the photosynthesis and transpiration, photosynthesis and WUE, as well as photosynthesis and precipitation (Table 4). Significant negative correlation was observed between leaf temperature and precipitation.

4 Discussion

A decreasing trend of photosynthesis during the summer growing season, from July to September, was obvious. During the investigated period, a shortage of precipitation was measured on Fruška gora mountain, and on the basis of our results, which indicated positive significant correlation between photosynthesis and precipitation (0.72*), we can conclude that photosynthetic depression was caused by drought environmental conditions. Lack of precipitation was not correlated with soil water capacity, but rather with a multi-month absence of water in deeper layers of soil. Therefore excess of precipitation in May and June as well as accumulated water in deeper layers

Table 4. Correlation between monthly averages of investigated parameters (*p < 0.05)

	P	T	WUE	Tl	Precipitation
P	1	0.98*	0.92*	0.28	0.72*
T	0.98*	1	0.84*	0.28	0.75
WUE	0.92*	0.84	1	0.26	0.57
Tl	0.28	0.28	0.26	1	-0.37
Precipitation	0.72*	0.75*	0.57	-0.37	1

*Correlation significant for *p < 0.05

of soil caused high and stabile photosynthesis in July. The reduction of photosynthesis caused by drought occurrence in vegetation period was certainly expected and previously confirmed in many studies [15-17]. Comparing the monthly averages of photosynthesis, it could be seen that the highest photosynthetic production was found in July, when the average temperature was about 25.5°C.

Daily photosynthesis of beech leaves showed rhythmical changes. It was the most intensive in the morning (around 9 am), it decreased between noon and 1 pm, and it increased again during the early afternoon. These two peaks of photosynthesis are recognized as typical diurnal photosynthetic dynamics of some woody plants measured during the daily climatic variation [18], and also during severe drought [19,20]. Similar rhythmical changes in the net photosynthetic rate were also observed for herbaceous plants: an early morning maximum, then a pronounced midday depression and a subsequently small recovery late in the afternoon [21,22]. The midday depression could be explained by significant and negative correlation between photosynthesis and weather conditions like high temperature, as well as a shortage of precipitation. Soil moisture deficits are often associated with high temperatures causing peak rates of daytime carbon dioxide uptake to occur earlier in the morning in broad-leaved forests [23]. High temperature and absence of precipitation in 2012, several weeks before our measurements on mountain Fruška gora, caused a brief inactivation and depression of photosynthesis at midday. During the day the highest values of photosynthesis were measured when the temperatures of the leaves were between 23.5 and 25°C.

Positive and significant correlation between monthly average transpiration and gs was determined. Similar results were also recorded in other articles [24]. Macfarlane *et al.* [25] observed that stomatal conductance and the rate of net photosynthesis were highly correlated, and declined together with the rate of transpiration throughout the afternoon as vapor pressure deficit of ambient air increased, despite increasing leaf water potentials.

Our findings indicated that WUE is correlated with photosynthesis and transpiration, and it had two maximums during the day: one in the morning, and one in the early afternoon. Positive and significant correlation between these three parameters was observed. Significant and positive correlation with the gs and temperature was also defined during the day. Due to permanent low precipitation levels during July, August and September, the continuous decreasing of WUE was observed.

Significant positive correlation between the stomatal conductance and the rate of photosynthesis was also observed. Higher photosynthetic CO_2 assimilation is the result of good stomatal conductance for gas exchange during photosynthesis. Midday depression of stomatal conductance and related depression of photosynthesis were determined in other studies as well [24]. These authors also observed that stomatal conductance is higher in the morning relative to the gs in the afternoon, and this can be explained with the lower leaf water potential in the afternoon resulting from a higher atmospheric demand and a reduced ability of the soil to supply water to roots due to lower matrix potentials and hydraulic conductivity. Aranda *et al.* [26] stated that decline in leaf specific hydraulic conductance of some woody plants was followed by an increase in stomatal control of daily water losses through the decrease of stomatal conductance to water vapor during the day. It provokes a seasonal increase in the stomatal limitation to carbon dioxide uptake for photosynthesis. This maintenance of the hydraulic function had a negative impact on the tree carbon balance because net photosynthesis was also depleted. The role of the hydraulic control in stomatal closure has been identified in trees [27-29]. In our study, the significant decrease of photosynthesis was observed at noon. Leaf temperature (Tl) or the ratio of air to leaf vapor pressure deficit is the determinant factor of midday depression of photosynthesis [30]. Macfarlane *et al.* [25] found that leaf water potentials of *Eucalyptus globulus* declined until late morning, but began to increase from about midday leading to stomatal closure. Results of citrus investigations determined that photosynthesis was highly responsive to changes of gs and the depression of P in summer resulting from an increase of temperature [31]. In our investigation, the significantly negative correlation between the Tl and gs was observed only in September. We assume that the reason for this result is that the shortage of precipitation on the investigated locality became critical only at the end of the growing season. Dai *et al.* [32] suggested that the increase of ALVPD (air to leaf vapor pressure deficit) associated with rise of Tl might cause the decrease of gs at *Ricinus communis*.

Drought can significantly change stomata density, depending on the degree and duration of water deficit and observed plant species. Many studies have shown that drought stress leads to an increase in stomata density, followed by a decrease in stomata size as an xeromorphic adaptation strategy to water deficit [33,34]. For *Fagus sylvatica* it has been suggested that increased stomata density could be an adaptation to physiological risk of water stress [35,36]. Our results also indicated that stomata density had been affected by water deficit. Stomata number per mm^2 of leaf area was the highest in September, followed by a decrease of stomata conductance, which indicated that stomata were oftentimes closed. Increase in stomata density in grass [37] and lentil [38] was determined by moderate drought stress, although this increase was reversed under severe drought conditions. Also, some results are showing drought induced reduction of both stomata density and size [39,40]. Although the number of stomata in our investigation was increased by water deficit, the expected decrease of stomata size was not detected.

The amount of the photosynthetic pigments did not significantly change during the investigated period, because the leaves were not in the senescence phase. In September, there were no evident signs of early leaf senescence on the trees and the temperature was not sufficiently high to cause thermal degradation of the photosynthetic pigments. We didn't find any correlation between the content of photosynthetic pigment and environmental temperature, in contrast to some other works where results indicate that content of photosynthetic pigments increased due to warmer temperatures [41].

Soil water capacity measured in the 30 cm layer did not show a significant decreasing trend from July to September, but decline in photosynthesis and transpiration suggested that this parameter contributed to the photosynthesis until the end of vegetation season. We assume that the measured soil water capacity calculated from the samples taken from the soil depth of 30 cm is not an adequate indicator because even little precipitation might cause changes, and this is why extensive drought could not be identified in the soil. Beech trees have deep, extensive roots, and low sporadic precipitation could not increase humidity in the deeper soil layers, due to quick surface evaporation caused by the high temperatures. This is supported by the findings showing that 15% of young beech trees with a diameter less than 30 cm dried at the measuring locality on Fruška gora 2012th.

After analyzing the obtained data, we can conclude that the beech forest showed some adaptation response to drought and temperature stress. However, extensive periods of low precipitation significantly reduced the level of CO_2 assimilation, therefore decreasing its ability to significantly reduce atmospheric CO_2 levels. A decreasing trend of photosynthesis of beech plants when shortage of precipitation was measured during the investigated period indicated positive significant correlation between photosynthesis and precipitation. Diurnal photosynthetic rhythm is also correlated with daily climatic variation.

Therefore, monitoring of physiological parameters could be important for defining forest ecological conditions. Physiological status, linked to primary photosynthetic productivity of forests, could be a significant indicator of environmental conditions and climate changes.

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Conflict of interest: Authors declare nothing to disclose

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