EFFECTS OF DROUGHT ON SELECTED PHYSIOLOGICAL PARAMETERS OF YOUNG BEECH TREES UNDER STRESS CONDITIONS

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Abstract

Ditmarová Ľ., Kmeť J., Střelcová K., Gőmőry D.: Effects of drought on selected physiological parameters of young beech trees under stress conditions. Ekológia (Bratislava), Vol. 25, No. 1, p. 1–11, 2006.

We studied physiological characteristics (fluorescence of chlorophyll *a*, photosynthetic pigments) in shade leaves of beech (*Fagus sylvatica* L.) trees in dependence on one- and two-week precipitation totals (in mm) before the proper measurement and sampling, in two areas with different pollution load. The leaf characteristics were observed on 15 year old understorey trees.

From the results it follows that both short-term and long-term deficit in precipitation were more sensitively responded by the measured fluorescence parameters than by the amounts of the assimilatory pigments. This primarily holds for the two-week precipitation totals. In the locality more loaded by airborne pollutants, the influence of drought in coupling with other negative site factors results in worse physiological state of beech trees.

Key words: drought stress, stress physiology, chlorophyll fluorescence, pigment content, Fagus sylvatica L.

Introduction

Availability of water is one of the factors determining the volume and parameters of biomass production over the Earth's surface. In the case of limited water availability and under deficit in precipitation water (the demands determined by the evaporation are dominant), the soil becomes to over-dry. The plant (that means also the woody plant) water conditions are dependent on the water uptake by the root system and on the water loss in transpiration - the output component of the water transport in the system soil - plant - atmosphere. Any

drop in the groundwater supply can lead to a change in the water conditions in woody plants and some extent of the dehydration of tissues (Střelcová, Kmeť, 2003).

Drought or water deficit in woody plants cause a disturbance of water balance and disproportion between the water uptake and the water demands during the ontogenesis. Under semi-arid conditions, water deficit is a frequently occurring phenomenon. Trees and shrubs cope with the problem according to the degree of their resistance or tolerance. Water stress in plants can also be induced through ecological interactions. The signals of this stress can be monitored and expressed by both belowground and aboveground organs whose temporal and spatial performance is quite strictly defined. However, the perception of a stress signal need not mean that the trees suffer from water deficit. The issue is complex and requires precise definitions of such concepts as drought, water deficit, water stress - frequently interchanged in plant physiology (Brestič, Olšovská, 2001).

The question arises whether the adaptation changes associated with drought in woody plant species are primarily driven by a drop in soil water potential or by the stress accompanying the water deficit in woody plants. Important is also the registration of drought signals in the plant tissues. A plant exposed to a moderate stress activates its regulation and adaptation mechanisms ensuring the regeneration of stress-damaged enzymes and the transport of water, nutrients and other metabolites to plant parts with higher metabolic activities. In the case when the stress is severe, irreversible disturbances in the metabolism arise, basic processes of water uptake and output are inhibited, the leaf apparatus is damaged etc. It is evident that the plant water economy also affects the biomass production in the photosynthetic processes. Obviously, the mechanisms and control of photosynthesis have for long been intensively studied. It is a process with a key importance from the viewpoint of biomass production.

The precipitation shortage recently occurring over the majority of the Slovak territory can negatively influence the moisture insurance, health state and yield of forest tree species not only in the lower forest vegetation tiers with the predominance of oaks (fvt 1–3), but also in the communities with prevailing beech (fvt 4–6) and the communities of the higher forest vegetation tiers dominated by spruce (fvt 6–8) (Škvarenina et al., 2002). The water regime of the soils in the mountain range (fvt 6–8), especially their very low water-retention capacity, is considered a crucial factor during the periods of climate changes and extremes. For the plant physiology, the precipitation shortage is especially unfavourable in July and August. It must be noted that, in the past years, over the majority of the Slovak territory, the maximum mensual precipitation totals within the annual course were generally reached in July (Priwitzer et al., 2003).

The aim of this work was to evaluate the influence of the precipitation total (one and two weeks before the sampling) on selected physiological and biochemical parameters of assimilatory organs of beech trees growing at two localities under different air-pollution loads and to asses the effect of the drought as a stress factor on the deterioration of the physiological state of this tree species (short-term and long-term stress effect).

Materials and methods

The first experimental plot is located in the forest stand No. 289, which is situated in the Žiarska kotlina (north of the Štiavnické Mts) near an Aluminium plant, Žiar nad Hronom (Central Slovakia). The second plot belongs to the Ecological Experimental Site (EES) of the Institute of Forest Ecology situated in the Kremnické Mts. A detailed description of the plots can be found in our previous paper (Ditmarová, Kmeť, 2002) (Table 1).

Characteristic	Resear	ch plot
	EES Kováčová	VMP Žiar nad Hronom
Location	Kremnické vrchy Mts	Štiavnické vrchy Mts
Exposition	West	Northwest
Altitude (m a.s.l.)	450-475	400
Stand age (years)	12	12
Stocking	0.0-0.5	0.6
Area	0.15	0.21
Parent rock	dark pyroxene andesites,	rhyolitic agglomerates
Soil type	volcanic sandstones, tuffs cambisol with high content of skeleton	luvic pseudogleyic cambisol
Group of forest types	Fagetum pauper nst.	Querceto-Fagetum
Average annual temperature [°C]	6.8	7.6
Average annual precipitation [mm/year]	778	750
Distance from emission source [km]	18	1.5

T a ble 1. Basic characteristic of the research plots

EES - ecological experimental stationary plot, VMP - research monitoring plot

At both localities, five individuals of beech (*Fagus sylvatica* L.) were selected, aged approximately 15 years (in 1996). The sample trees were situated under the canopy. The sampling did not include trees growing on the research plot boundary and near the footpaths. During the growing seasons 1996-2000, assimilatory organs from beech trees were collected at both localities always on the same day of the respective year. For each year the plant material was sampled 8-10 times (from May to October). In total, 33 measurements were accomplished.

Chlorophyll a fluorescence measurement: We measured the chlorophyll fluorescence on two branches from each individual sample tree. Measurements were carried out both on the adaxial and abaxial leaf sides. To determine the parameters of rapid kinetics of chlorophyll *a* fluorescence (F_0 , F_m , F_v , F_v/F_m , *Area* - nomenclature by Kooten, Snel, 1990), we used a portable fluorometer (Plant Efficiency Analyser - PEA, Hansatech Ltd., Kings Lynn, UK). A recording interval of 1 second was chosen. Before the measurement, leaves were kept for 30 minutes for dark adaptation under leaf clamp cuvettes. Measurements were performed at a 50% level of light energy saturating intensity (2100 µmol m⁻² s⁻¹).

Prior to each series of measurements of chlorophyll a fluorescence we carried out a preliminary testing measurement with the aim to determine the minimum time interval for dark adaptation for individual plants in

the given site conditions. The examined beech leaves were provided with 20 leaf clips. The clips were shut and the values of fluorescence of chlorophyll *a* were determined at various time intervals between one and 40 minutes. We used saturating light at a level of 100%. We have tabulated the data on assimilation organs adaptation in dependence on the ratio F_{a}/F_{m} . This ratio should attain its peak at the end of the minimum period necessary for the dark adaptation. After determining the time necessary for dark adaptation, we placed 10 leaf clips on leaves on the examined trees. The clips were left open for minimum time necessary for dark adaptation (in our case 30 minutes). The measurements were performed on each clip separately, at light intensity growing from 10 to 100%. The ratio F_{a}/F_{m} should attain its peak after exceeding the saturation point – in our case at 50%. In such a way, we had determined the saturating light intensity in μ mol m⁻² s⁻¹. It is commonly accepted that the 100% intensity of the saturation light is not connected with problems – supposing that the concentration of chlorophyll *a* is sufficiently high (Hansatech, 1993).

The proper measurements were carried out directly in field *in situ* on beech sample trees, around the whole perimeter of the medium crown part (related to tree age and material sampling for pigments analysis).

The parameters of chlorophyll a fluorescence were determined using a PEA fluorometer (Hansatech, Norfolk, England). The instrument is fully equipped and requires no supplementary facilities. It is a light in weight (1.5 kg), compact and easy portable system performing calculations automatically and saving the results in the memory.

The measurements with the apparatus are explained in details in Kmef (1999). We only give here a rudimentary description: plastic leaf clips are fixed at spots of leaf measurements and during 30 minutes these spots are darkened. During the measurement, the sensor unit is kept at the open lock of the clip. The sensor unit comprises diodes (LEDS) emitting red light and providing saturating concentrations (in μ mol m⁻² s⁻¹) for a time of 1 s. A rechargeable pile is sufficient to cover low energy demands connected with daylong recordings. The circuits controlled with a microprocessor guarantee precision and reliability of the results. The recorded data are background for automatic calculation of parameters of rapid kinetics of chlorophyll *a* fluorescence. It is also possible to count out these data from the liquid crystals on the display and to save them in the memory.

The method is based on the fact that the amount of light energy representing the surplus of demands by photosynthesis is dissipated in form of fluorescence or it is transformed to heat. The changes in rate of photosynthesis or in rate of dispersed heat are reflected in total changes in fluorescence emission. If all reaction centres of the photosystem II (RC PSII) are closed, then 95–97% of the absorbed energy is transformed to heat and 2.5–5% to fluorescence (Bolhar-Nordenkampf, Öquist, 1993). If the assimilation organ is exposed to a sudden light (after previous dark adaptation), the examined fluorescence induction curve is time-dependent (effect of Kautský). A detailed description of the measuring equipment is given in Kmet (1999).

Quantitative analysis of pigments: Chlorophyll analyses were carried out in 80% acetone extracts. The chlorophyll a, b and a+b contents of the extracts were determined spectrophotometrically and calculated according to Lichtenthaler (1987). The concentrations of the chlorophyll a, chlorophyll b and chlorophyll a+b were related to the dry-mass unit (mg.g⁻¹) and leaf area unit (mg.dm⁻²).

Statistical evaluation of the results: The drought stress was assessed as the precipitation amount summed over 7-days and/or 14-days period before the day of measurement of physiological traits (Fig. 1). Shorter periods were not considered, because we assumed that, e.g., one or two days without rain cannot induce a stress reaction. On the other hand, the precipitation amounts within a long period, e.g., one month, would probably be balanced, so no relationships were expected. The days of measurement were omitted, because of the possible effect of rain occurring after the measurement of physiological traits was performed. Precipitation values were obtained from daily measurements at the standard meteorological stations Sliač (Kremnické vrchy Mts) and Žiar nad Hronom (Žiarska kotlina basin), which are the most closely located to sample plots.

If the calculated drought parameters actually reflect the stress level, then the relationships between the measured physiological traits and drought parameters should be monotonous (the stronger is the stress, the stronger is the physiological response). However, the response need not necessarily be linear. Therefore, these relationships were assessed and tested using Spearman's rank correlation coefficients. SAS STAT[®] program package (SAS Institute, 1988) was used for the calculations.

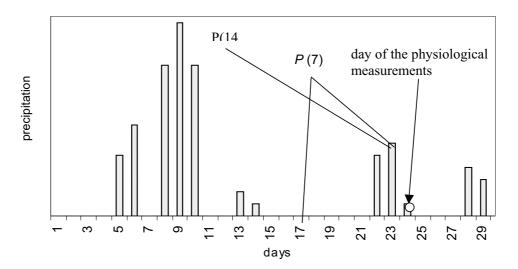


Fig. 1. Illustration of the definition of the drought stress indicators – precipitation totals during a one-week (P(7)) and/or two-week (P(14)) period before the day of physiological measurements.

Results

As we were focused on the influence of precipitation deficit on selected physiological traits and biochemical parameters of shade leaves of young beech trees, we present in Fig. 2 characteristics of precipitation history over vegetation periods 1996–2000, recorded at the meteorological station Sliač. The deviations of month's totals from the 30-year average

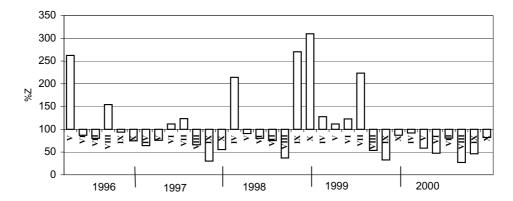


Fig. 2. Illustration of the definition of the drought stress indicators – precipitation totals during a one-week (P(7)) and/or two-week (P(14)) period before the day of physiological measurements.

over the period 1951 to 1980 are expressed as percents, and they indicate that a remarkable moisture deficit occurred during the vegetation period of 1998 (May to August) when there was a 90 mm lack in precipitation compared to the long term average. The year 2000 was extremely dry, with the precipitation deficit 142 mm in the period May to August. In terms of physiology, the years 1996, 1997 and 1999 can be classified as years with sufficient water supply during the vegetation period. Precipitation deficit in years 1998 and 2000 was mainly reflected in the parameters of chlorophyll fluorescence (F_{var} , *Area*) at the locality EES in the Kremnické vrchy Mts with lower values compared to years 1996, 1997 and 1999. At the locality Žiarska kotlina basin, this phenomenon was not observed.

The interactions between the studied physiological parameters and the drought-stress indicators (precipitation totals within one and/or two weeks before the physiological measurement) were assessed by Spearman's rank correlation coefficients.

T a b l e 2. Spearman's rank correlation coefficients between chlorophyll fluorescence parameters in beech leaves (adaxial leaf side) and precipitation at the site EES Kremnické vrchy Mts

Precipitation	F_{o}	F_{m}	F_{r}	F/F	T_{m}	Area
ZT	-0.02495	0.07596	0.10006	0.15540°	-0.21608**	-0.00702
Z2T	0.19186 [.]	0.27256***	0.26890	0.18192	-0.14532	0.22761

ZT – one-week precipitation totals [in mm] before the day of measurement and sampling Z2T – two-week precipitation totals [in mm] before the day of measurement and sampling p < 0.05, "p < 0.01, "p < 0.001

Table 2 shows a statistically highly significant positive effect of the two-week precipitation total (Z2T) on the values of maximum (F_m) and variable (F_v) fluorescence on the adaxial side of assimilatory organs of beech trees growing in the locality EES Kremnické vrchy Mts. A similar effect of this factor on the fluorescence parameters on the abaxial leaf side was observed (Table 3), along with a highly significant influence of the two-week precipitation total on the parameter *Area* (the area above the induction curve of fluorescence between the values F_o and F_m), what may partly indicate negative physiological effects of the precipitation deficit (lower precipitation total leads to lower values of the parameter *Area*, and thus a lower amount of electron acceptors on the reduction side of PS II).

T a b l \in 3. Spearman's rank correlation coefficients between chlorophyll fluorescence parameters in beech leaves (abaxial leaf side) and precipitation at the site Žiarska kotlina basin

Precipitation	F_{o}	F_{m}	F_{ν}	F./F.,	T_{m}	Area
ZT	0.03054	0.11212	0.11541	0.17117	-0.08833	0.07896
Z2T	0.17322	0.29040***	0.28864***	0.19758**	-0.01685	0.29388***

p < 0.05, p < 0.01, p < 0.001

The sign and the significance level of the calculated Spearman's coefficients of rank correlation allow us to conclude that the given precipitation totals had also significant effects (significance levels *p < 0.05 and **p < 0.01) on the principal parameter of chlorophyll fluorescence - the ratio of variable and maximum fluorescence (F_{γ}/F_{m}). Consequently, it means that primarily a low two-week precipitation total can cause this parameter to drop even to the level of physiological disturbances (0.725).

At the locality EES Kremnické vrchy Mts, the lowest one-week (ZT) and two-week (Z2T) precipitation totals over the whole study period were measured on September 30, 1997 (0 mm, 0 mm), September 22, 1999 (1.2 mm, 1.2 mm), September 6, 1999 (4.5 mm, 4.5 mm), and September 5, 2000 (6.9 mm, 6.9 mm).

A similar influence of the precipitation total on the studied parameters of the rapid phase of fluorescence induction phenomenon was observed both for the adaxial (Table 4) and abaxial (Table 5) side of assimilatory organs in beech trees growing at the locality under unfavourable environmental conditions – loaded with airborne pollutants (Žiarska kotlina basin). At this locality, two-week precipitation totals also exhibit more significant effects (mainly for the parameters measured on the adaxial leaf side).

T a b l e 4. Spearman's rank correlation coefficients between chlorophyll fluorescence parameters in beech leaves (adaxial leaf side) and precipitation at the site EES Kremnické vrchy Mts

Precipitation	F_{o}	F_{m}	F_{v}	<i>F</i> ./ <i>F</i>	T_{m}	Area
ZT	0.02564	0.02936	0.04335	0.03712	-0.22366**	-0.00566
Z2T	0.24904**	0.29684	0.30780***	0.23941	-0.12310	0.29239

p < 0.05, p < 0.01, p < 0.001

At the locality Žiarska kotlina basin, the lowest one-week (ZT) and two-week (Z2T) precipitation totals over the whole study period were measured on September 30, 1997 (0 mm, 0 mm), September 22, 1999 (1.8 mm, 1.8 mm), August 25, 1997 (1.3 mm, 2.8 mm), September 5, 2000 (5.5 mm, 5.5 mm), and September 6, 1999 (6.1 mm, 6.3 mm).

T a b l e 5. Spearman's rank correlation coefficients between chlorophyll fluorescence parameters in beech leaves (abaxial leaf side) and precipitation at the site Žiarska kotlina basin

Precipitation	F_{o}	F_{m}	F_r	F./F.,	T_{m}	Area
ZT	-0.17601	-0.13099	-0.09929	0.11156	-0.12142	0.04970
Z2T	-0.00717	0.10394	0.11038	0.19701.	-0.08174	0.26754

p < 0.05, p < 0.01, p < 0.001

An interesting outcome is a negative correlation between the precipitation total and the content of assimilatory pigments converted either per weight (mg.g⁻¹) or per area unit (mg.dm⁻²) of beech leaves, although it is non-significant almost in all cases. This relation-

T a b l e 6. Spearman's rank correlation coefficients between photosynthetic pigments and precipitation at the site EES Kremnické vrchy Mts

Precipitation	Chl a	Chl b	Chl a+b	Chl a/b	Chl a	Chl b	Chl a+b
	$[mg.g^{-1}]$	$[mg.g^{-1}]$	$[mg.g^{-1}]$		[mg.dm ⁻²]	[mg.dm ⁻²]	[mg.dm ⁻²]
ZT	-0.13379	-0.06100	-0.11270	-0.10289	-0.02528	0.07404	0.00510
Z2T	-0.11436	0.02310	-0.07721	-0.21633**	0.02973	0.15268	0.06750

p < 0.05, p < 0.01, p < 0.001

ship indicates that in association with the other site conditions (pollution load, temperature, solar radiation), the influence of precipitation deficit on the photosynthetic pigments concentration disappears (stimulating influence of site conditions on pigments concentrations). This finding holds for both studied localities - EES Kremnické vrchy Mts and Žiarska kotlina basin (Table 6 and 7).

T a b l e 7. Spearman's rank correlation coefficients between photosynthetic pigments and precipitation at the site Žiarska kotlina basin

Precipitation	Chl a	Chl b	Chl a+b	Chl a/b	Chl a	Chl b	Chl <i>a+b</i>
	$[mg.g^{\cdot i}]$	$[mg.g^{\cdot i}]$	$[mg.g^{\cdot i}]$		[mg.dm ²]	[mg.dm ²]	[mg.dm ⁻²]
ZT	-0.12836	-0.10899	-0.12377	-0.08219	-0.05007	-0.01437	-0.04540
Z2T	-0.11966	-0.02835	-0.09058	-0.19027*	-0.00377	0.08447	0.01660

p < 0.05, p < 0.01, p < 0.001

From our results, it follows that both short-term and long-term deficit in precipitation were more sensitively reflected in the measured parameters of chlorophyll fluorescence than in the observed assimilatory pigments contents. Primarily in the case of the locality more loaded with airborne pollutants (Žiarska kotlina basin), drought, in combination with other negative site factors, leads to the deterioration of the physiological state of beech trees.

Discussion

Recently, a special attention was devoted to the tolerance and symptoms of damage to beech trees in various environmental conditions and under different pollution load. However, both in Slovakia and abroad, a more complex research of the dynamics of damage to beech ecosystems is more or less an exception. A large number of various problems in theory and practice (Vacek, 1993; Ditmarová, Kmeť, 2002) are to be answered, considering methodological problems and also a wide variety of pollution and ecological conditions.

In the context of stress-influence of airborne pollutants on forest woody plants, there is also important role of extreme values of various climate factors, primarily high and low temperatures, excessive FAR or drought. All these factors cause a reduced resistance of woody plants against the existing stress load.

The principal parameter of the rapid phase of chlorophyll fluorescence kinetics - the ratio of the variable to the maximum fluorescence (F_{\checkmark}/F_m) - is in general considered to be a good marker of the physiological stress in plants because it appropriately reflects the quantum yield of PSII. A relatively high resistance of PS II (Epron, Dreyer, 1990) against dehydration has been confirmed for several plant species with different tolerance to drought and/or for different species of plants belonging to C3 group. The cited work outline the difficulties connected with the distinguishing between the specific effects of the water deficit on the photosynthetic apparatus and the secondary effects induced by drought or by interactions with other factors limiting other physiological processes.

The results obtained in experiments with the rapid dehydration have revealed that the rate of induction of non-photochemical quenching $q_{\rm NP}$ had not been lowered down to the level of 50% water saturation deficit - WSD (Schreiber, Bilger, 1987). This result supposes a disturbance in the electron transport capacity caused by inhibited consummation of the reduction factor. PSII intact state and stability in the electron transport chain also meant an intact state and stability of the cell membranes what also was confirmed in the measurement of released electrolytes at a dehydration exceeding 60% WSD (Brestič, Olšovská, 2001). Under the conditions of a severe water stress, the transport of electrons though PSII is inhibited which is finally also reflected in the fluorescence parameters.

Peuke et al. (2002) assessed the effects of drought on European beech in a pot experiment under controlled conditions. Plants from 11 autochthonous provenances originating from regions in Germany, which differed in annual precipitation, were exposed to a 3week drought period in a greenhouse, after the first stage of their shoot growth had been completed. The drought reduced the water content to 97% in leaves and axes and to 92% in the roots. A strong reduction of predawn water potential in roots and shoots, as well as of transpiration rate, was found. Two extreme clusters from opposite climatic sites were identified by cluster analysis. A drought-sensitive cluster, corresponding to regions with high annual precipitation, had low water potential and transpiration rates, as well as high concentrations of fructose, ABA and proline after drought. Water potential and transpiration rates were less affected by drought and concentrations of hexose, ABA and proline were low, in the other cluster, which covered two provenances of relatively dry habitats.

The dynamics of the chlorophyll content in plant assimilatory organs is influenced by several site environmental factors (natural seasonal changes in the chlorophyll content, differences between sun and shade leaves, airborne pollutants, drought, extreme temperatures etc.). This explains frequently reported contradictory results considering not only the concentrations of the individual pigments but also their relative proportions (Mikkelsen, Heide-Jorgensen, 1996).

Šesták (1985) means that the water stress causes a lowered rate of photosynthesis (P_N), by limiting the CO₂ transport in both gaseous and liquid phase into the chloroplasts and by hampering, in such a way, the biochemical activity of the chloroplasts. It follows that the influence of water stress on photosynthetic production is very complex.

Masarovičová et al. (1996) found that the water retention capacity, i.e. also the resistance against drought, was higher in beech leaves at the locality EES Kremnické vrchy Mts compared to Žiar nad Hronom. In the second locality, this mechanisms is impaired, probably as a consequence of the airborne pollution impact. At both plots, a higher water retention capacity was observed in sun leaves, the lowest in the leaves on understorey trees. This difference was the most evident in long periods of drought.

Physiological response to drought in beech seedlings from two Italian populations and the possibility of their regeneration was examined (based on the analysis of chlorophyll content, chlorophyll fluorescence and photosynthesis) by Tognetti et al. (1995). The authors found that the increasing water stress entailed decreases in water potential, in relative content of water in leaves, in the net rate of photosynthesis and in chlorophyll content. On the other hand, they did not observe any change in the relative fluorescence.

Conclusion

The trend of climate change over the last one hundred years indicates a permanent decrease in the annual totals of atmospheric water precipitation and a decrease in mean annual values of air relative humidity. Evident is a simultaneous increase in the mean annual values of air temperature entailing increasing evapo-transpiration demands on water. Dry periods between the precipitations events are getting longer which causes that the plants often suffer from water shortage. The water stress (more precisely the stress caused by the drought) becomes to be the leading abiotic stress-factor limiting the growth and productivity of plants on the Earth. That is why also eco-physiologists are required to devote to the problem intensive and thorough attention.

Translated by D. Kúdelová

Acknowledgement

This work was financially supported by the Grant 2/4159/04, 1/9207/02, 1/0629/03 and Grant 2/4167/24, from the Grant Agency of the Slovak Republic.

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Received 18. 5. 2004

Ditmarová Ľ., Kmeť J., Střelcová K., Gömöry D.: Analýza vplyvu sucha na vybraté fyziologické parametre mladých jedincov buka v stresových podmienkach.

V rámci uvedeného príspevku sme sledovali fyziologické charakteristiky (fluorescenciu chlorofylu *a*, fotosyntetické pigmenty) tiennych listov buka (*Fagus sylvatica* L.) vo vzťahu k 1-týždňovým a 2-týždňovým úhrnom zrážok v mm pred vlastným meraním a odberom vzoriek z oblastí s rozdielnou imisnou záťažou. Charakteristiky listov sme sledovali u podrastových jedincov vo veku 15 rokov.

Z výsledkov vyplýva, že na krátkodobý a strednodobý vplyv deficitu zrážok citlivejšie reagujú parametre fluorescencie chlorofylu ako obsah asimilačných pigmentov. Platí to predovšetkým pre dvojtýždňové úhrny zrážok. Na lokalite imisne zaťaženej (Žiar nad Hronom) vplyv sucha v kombinácii s ďalšími negatívnymi stanovištnými faktormi môže byť v konečnom dôsledku príčinou zhoršeného fyziologického stavu buka.