Lesn. Cas. For. J. 60 (2014) 31–37

PÔVODNÁ PRÁCA – ORIGINAL PAPER

Lesnícky časopis -
Forestry Journal
http://www.nlcsk.sk/fj/

Photosynthetic response of European beech to atmospheric and soil drought

Fotosyntetická reakcia buka lesného na atmosférické a pôdne sucho

Tibor Priwitzer[1*], Daniel Kurjak[2, 3], Jaroslav Kmeť[2], Zuzana Sitková[1], Adriana Leštianska[2]

[1]National Forest Centre - Forest Research Institute Zvolen, T. G. Masaryka 2175/22, SK – 960 92 Zvolen, Slovakia
[2]Technical University in Zvolen, Forestry Faculty, T. G. Masaryka 24, SK – 960 53 Zvolen, Slovakia
[3]Czech University of Life Sciences Prague, Faculty of Forestry and Wood Sciences, Kamýcká 129,CZ – 165 21 Praha 6 - Suchdol, Czech Republic

Abstract

Physiological response of European beech under soil and atmospheric drought conditions was investigated in this study. A group of six beech trees was irrigated during the growing season 2012, while the second group of non-irrigated (control) beech trees was treated under natural soil drought. During the experiment, we observed more than 45-day long period when no precipitation fell on the soil surface. The relationship of P_N (CO_2 assimilation rate) to g_S (stomatal conductance) was very tight in both groups, which indicates that stomatal opening was the main factor limiting P_N. The statistically significant differences in g_S between the groups of trees were revealed only on the last measuring day. The significant differences in P_N were confirmed on the days when the differences in soil water potential (Ψ_S) appeared. On these measurement days, the P_N values of irrigated individuals were approximately 1.9 or 3.3 times greater than the values of non-irrigated individuals. At the level of primary photosynthetic processes (chlorophyll fluorescence parameters) we did not observe lower values of the control individuals in comparison with the irrigated trees in any of the evaluated parameters. Long-term soil water deficit caused strong decrease of leaf water potential (Ψ_L) in the control trees, but Ψ_L values of the irrigated trees were also rather low due to diurnal dynamics in higher parts of crown. Close relationship between Ψ_L and g_S was confirmed for the control (non-irrigated) trees, but could not be confirmed for the irrigated trees. We revealed significant influence of *VPD* (vapour pressure deficit of the air) on g_S only in the control group. On the days when Ψ_S decreased, the stomata of the non-irrigated trees were closed in spite of the low *VPD* values. Almost complete stomatal closure in both groups of trees was caused by the increase of *VPD* to 1.2 kPa.

Keywords: *Fagus sylvatica;* water deficit; vapour pressure deficit; leaf water potential; stomatal closure

Abstrakt

Príspevok sa zaoberá skúmaním fyziologických reakcií buka na atmosférické a pôdne sucho. Skupina šiestich bukov bola zavlažovaná počas vegetačnej sezóny 2012, pričom druhá skupina bukov (kontrola) bola ponechaná v prirodzených pôdnych vlahových podmienkach. Počas experimentu bola pozorovaná viac než 45 dní trvajúca perióda, kedy sa zrážková voda nedostala na povrch pôdy. Potvrdili sme silnú závislosť rýchlosti asimilácie (P_N) na prieduchovej vodivosti (g_S), čo dokazuje, že otvorenosť prieduchov bola hlavným limitujúcim faktorom priebehu asimilácie CO_2. Štatisticky významné rozdiely g_S medzi skupinami boli potvrdené len počas posledného merania. Významné rozdiely v P_N sa potvrdili predni, v ktorých sme zistili výrazné rozdiely vo vodnom potenciáli pôdy (Ψ_S). Počas týchto dní boli priemerné hodnoty P_N pre zalievané stromy 1,9, resp. 3,3-krát vyššie v porovnaní s nezavlažovanými jedincami. Na úrovni primárnych fotosyntetických procesov (parametre fluorescencie chlorofylu) sme nezistili nižšie hodnoty kontrolných jedincov v porovnaní so zavlažovanými. Dlhodobý deficit vody spôsobil pokles vodného potenciálu listov (Ψ_L) kontrolných stromov. Potvrdili sme závislosť g_S na Ψ_L pri kontrolných jedincoch, nie však pri zavlažených. Vplyv deficitu tlaku vodných pár (*VPD*) významne ovplyvnil g_S len pri kontrolnej skupine. Počas dní, kedy poklesol Ψ_S, boli prieduchy nezalievaných jedincov zatvorené aj v prípade, že hodnoty *VPD* boli nízke. Takmer úplné zatvorenie prieduchov oboch skupín stromov bolo spôsobené nárastom *VPD* na hodnotu 1,2 kPa.

Kľúčové slová: *Fagus sylvatica*; stres zo sucha; deficit tlaku vodných pár; vodný potenciál listov; zatváranie prieduchov

Introduction

European beech (*Fagus sylvatica* L.) is one of the major broad-leaved tree species in forests of Central and Western Europe (Coll et al. 2004). In Slovakia, it represents 32.2% of the entire wood stock (Green Report, 2013). Beech grows in most forest stands of Slovakia from the lowlands (200–330 m a.s.l.) up to the mountains (1,260–1,480 m a.s.l.) (Pagan & Randuška 1987). In many regions of Europe, including Slovakia, growth conditions for European beech can be heavily affected by climate change. Rising intensities of individual precipitation events may result in reduced precipitation during the growing season and in a higher frequency of summer droughts. Growth and competitive ability of European beech may be strongly impacted by intensive drought that occurs during the growing season (Geßler et al. 2007). The impact of projected changes in frequency and intensity of occurrence of extreme climate events may in future be more profound than the changes in the average values of temperature and precipitation (Fuhrer et al. 2006).

The works dealing with drought impact on beech water regime and photosynthetic processes indicate that beech does not tolerate drought stress in spite of several mechanisms regulating the rate of water deficit (Fotelli et al. 2009; Bréda et al. 2006). Due to its wide European distribution

---

[*] *Corresponding author. Tibor Priwitzer, e-mail: priwitzer@nlcsk.org*

and its drought-susceptibility, beech has recently received intensive attention in the light of global warming (Fotelli et al. 2009) and several studies have focused on its response to limited water availability (Cochard et al. 1999; Bréda et al. 2006). Dry and hot weather during summer were found to strongly reduce net primary production of beech forests (Ciais et al. 2005). Extreme weather events (drought) may relatively fast weaken physiological conditions of populations and may lead to disease and insect outbreaks also in the regions that are generally suitable for the species (Mátyás et al. 2010; Innes 1992). Hydraulic failure via stomatal closure, resulting in carbon starvation and a cascade of downstream effects (McDowell et al. 2008) is probably one of the main mechanisms of tree vitality weakening. Stomatal closure is one of the first responses to drought and a dominant limitation of photosynthesis at mild to moderate drought events (Cornic 2000). Stomata generally close as the vapour pressure deficit of the air increases (Addington et al. 2004).

Under the climatic conditions of Central Europe, the trees are not equipped with sufficiently effective plant´s defence mechanisms or strategies that would allow them to survive drought without negative impacts on their physiological processes and consequently, on their growth and production (Ježík et al. 2011; Hlásny et al. 2011). To be able to specify the demands of individual tree species on water supply, it is necessary to know their response to different levels of drought stress, as well as to specify the symptom and the effects of drought on forest trees and stands. The determination of critical limits, when the trees begin to suffer from drought, still belongs to open research challenges.

Despite the fact that beech is the most common tree species in our conditions, only few extensive ecophysiological studies oriented at soil and atmospheric dry conditions have been performed on grown beeches directly in the conditions of forest stands. Detailed physiological experiments were performed mostly on seedlings growing under controlled or semi-controlled conditions (Jamnická et al. 2013; Tognetti et al. 1995). Therefore, the objective of this study was to investigate the basic physiological response of European beech under soil and atmospheric drought conditions. We anticipated that the leaf water potential (Ψ_L), stomatal conductance (g_S) and consequently CO_2 assimilation rate (P_N) would decrease with the increasing duration of drought and increasing vapour pressure deficit of the air (*VPD*). Next, we discuss the influence of Ψ_L and *VPD* on stomatal closure. We expected small or no decrease in maximal photochemical efficiency of photosystem II in non-irrigated (control) trees in comparison with irrigated trees.

2. Materials and methods

2.1. Site, stand and experiment design description

The experimental site Bienska dolina is situated in central Slovakia (Central Europe, 48°36'43''N, 19°03'39''E), at an elevation of about 450 m above sea level. The site belongs to the 3rd beech-oak altitudinal vegetation zone and to the forest site type management unit called fertile beech-oak woods. The experimental forest is 65 years old and is dominated by European beech (*Fagus sylvatica* L.) – 85%. The location is inside the natural occurrence of beech forests. Beside the beech, oak (10%) and larch (5%) occur in the tree species composition. The experimental plot is located on the eastern hillside (maximum slope 30%). According to WRB (FAO, 2006), the soil at the research plot is classified as Haplic Cambisol formed on volcanic parent material. The more detailed description of soil properties at Bienska study site is given in Sitková et al. (2014). The climate of the region is slightly warm and moderately humid, with mean July air temperatures of 16 °C (Landscape Atlas of the Slovak Republic, 2002). Based on the long-term data 1961–1990, the mean annual temperature and annual precipitation totals is 7.3 °C and 690 mm, respectively. In summer 2012, during the period of soil water deficit, irrigation was applied to a group of 6 beech trees. The daily irrigation volume of 3 m^3 water was applied to the soil surface in the stands from July to September, in the following terms: every second to third day during the period from 3.7. to 27.7.2012 and at daily interval during the gradation of drought period between 18.8.2012 and 9.9.2012 (Fig. 1). The total water amount of 96 m^3 water was applied on the soil surface, which is comparable with 820 mm of precipitation. The second group of 6 trees was treated under natural soil drought.

The measurement of stand characteristics showed that the average diameter both tree groups was comparable (diameter of non-irrigated (control) and irrigated trees was 32.0 cm, and 32.7 cm, respectively). Variability of diameters is slightly higher in the irrigated group of trees (Table 1).

The branches were taken from the upper third of the crown (around 20 m high) and physiological parameters were immediately measured. Measurements were performed four times during the period of the experiment (days are marked in Fig. 1) always between 8:00 and 11:30. The effect of daytime was minimized by alternating the measurements between the irrigated and non-irrigated (control) trees.

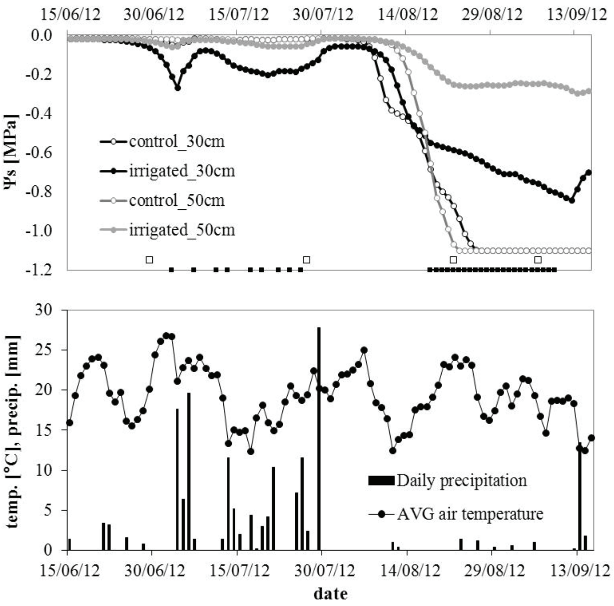

Fig. 1. Development of soil moisture at 30 and 50 cm depth at the irrigated and non-irrigated plots, daily precipitation and mean air temperature. The empty squares in the upper figure indicate days when physiological measurements were performed, while black squares indicate days when irrigation was applied.

Table 1. Height and stem diameter of 12 beech trees at Bienska dolina experimental site.

	Diameter of stem [cm]				Height [m]			
Group of trees	min	max	mean	std	min	max	mean	std
1–6 (control)	29.6	35.6	32.0	2.2	24.7	26.2	25.4	0.44
7–12 (irrigated)	27.1	42.3	32.7	6.0	25.5	29.1	27.1	1.19

2.2. Meteorological measurements

Meteorological parameters were measured at a nearby open area using a digital weather station (EMS Brno, Czech Republic). Air temperature (in degrees Celsius) was measured every 5 minutes by EMS33 sensor located at a height of 2 m. Precipitation was measured continuously, at 1 meter above the ground, using the raingauge with collecting area of 320 cm^2 and resolution of 0.2 mm per pulse (in millimetre; MetOne 370, USA). All measured data were stored as 20-minute averages in the datalogger EdgeBox V8 (EMS Brno, CZ). Soil moisture expressed as soil water potential (Ψ_s in MPa) was measured under forest canopy using standard measuring sets consisting of gypsum blocs and datalogger MicroLog SP3 (EMS Brno, CZ). Measurements were realized at three soil depths (15, 30 and 50 cm) and stored at 60-minute intervals. The acquired data were processed using Mini32 software (EMS Brno, CZ).

2.3. Leaf water potential measurement

Water potential (Ψ_L) of beech leaves was measured using Scholander-type pressure chamber (SAPS II, Soil Moisture Equipment Corp., USA). In total, 140 leaves were measured, while at least 3 leaves from each tree were measured per day. For each measurement date, mean values for each variant (irrigated and non-irrigated) were derived from at least five tree means calculated from the measurements of individual leaves.

2.4. Gas exchange measurements

CO_2 assimilation rate (P_N) and stomatal conductance (g_S) were measured on fully developed beech leaves using the LI-6400XT portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska) fitted with a 6400–40 leaf chamber. The measurements were performed on the detached branches. A standard 6 cm^2 of leaf area (projected) was enclosed in the leaf chamber. CO_2 concentration was kept at 385 ± 2 µmol mol^{-1}, saturating photosynthetically active radiation of beech was set to 1000 µmol m^{-2} s^{-1} (Masarovičová & Štefančík 1990) and temperature was set to 20 °C. Values were measured after short adaptation, after P_N values had remained stable. The vapour pressure calculation was based on leaf temperature. Ten values were recorded for each leaf, and 2–5 leaf values were averaged to obtain the mean for each tree. At least five irrigated and five non-irrigated trees were measured on each measurement date. In total, 160 leaves were measured.

2.5. Chlorophyll fluorescence measurements

Chlorophyll *a* fluorescence measurements were taken using a chlorophyll fluorimeter (Handy PEA, Hansatech Ltd, Kings Lynn, UK). The sample was irradiated by one-second-long saturating light pulse (approximately 3,000 µmol m^{-2} s^{-1}) after 30-min darkness adjustment. The following parameters were determined: F_v/F_m (maximal photochemical efficiency of PSII), F_v/F_0 (ratio of photochemical efficiency to non-photochemical efficiency; (Baker 2008). Performance index *PI* (plant vitality index reflecting the functionality of both photosystems II and I, (Strasser et al. 2000) was calculated from *O–J–I–P* fluorescence transient. Software package PEA Plus (Hansatech Ltd, Kings Lynn, UK) was used for *PI* calculation. Five leaf values were averaged to obtain the mean for each tree. For each measurement date, mean values for each variant (irrigated and non-irrigated) were derived from 5–6 tree means. In total, 225 leaves were measured.

2.6. Data analysis

The differences of physiological variables were tested using one-way ANOVA. Means were compared using Duncan's multiple range tests, at a significance level $P < 0.05$. The statistical analyses were performed using Statistica 7 (StatSoft, USA).

3. Results and discussion

The seasonal course of precipitation, daily mean air temperature and soil water potential (Ψ_S) at 30 and 50 cm soil depth on experimental site in 2012 is shown in Fig. 1. From May to August, the average monthly air temperatures were by 2.4 °C up to 3.4 °C higher than the long-term averages in 1961–1990. The precipitation totals of all months of the growing season except for July were below the long-term average data. In July, the long-term average of monthly precipitation totals was exceeded by 100%. The highest daily rainfall (27.8 mm) was recorded on 29 July 2012. Afterwards, a long lasting drought period with minimal daily precipitation and high air temperatures began. In August, the precipitation total was only 4.4 mm which is significantly below the long-term average for this region (65 mm). Due to the natural interception losses of the fully-stocked beech stand we presume that for more than 45 days no precipitation fell on the soil at the research plot. The precipitation totals at the experimental site during the vegetation period of 2012, i.e. from May to August, reached only 283 mm. Studies conducted in Bavaria by Felbermayer (1994) (in Englisch 2006) revealed that precipitation quantities of only 500 mm did not affect beech growth, although various authors indicate 500 mm as the minimum annual precipitation for Germany, 600 mm for Austria and 750 mm for France (Englisch 2006).

The seasonal course of soil water potential showed the decreasing tendency starting at the beginning of August on both the irrigated and non-irrigated parts of the plot. The critical values –1.1 MPa were recorded in the control group in the second half of August (Fig. 1). The decrease of Ψ_S in the irrigated group of trees ceased after 23 days of continual irrigation. The soil moisture conditions in the water-supplied part of the study forest were consequently improved and significantly differed between the treated groups (Sitková et al. 2014).

To test whether the changes in the CO_2 assimilation rate (P_N) were caused by the changes in stomatal conductance (g_S), assimilation rate was plotted against conductance (Urban et al. 2007). The relationship of P_N to g_S was very tight in both groups (Fig. 2), which indicates that stomatal opening was the main factor limiting the assimilation rate (not the failures at the level of the primary processes or other mechanisms). Similarly, Aranda et al. (2000) revealed tight correlation between P_N and g_S in beech.

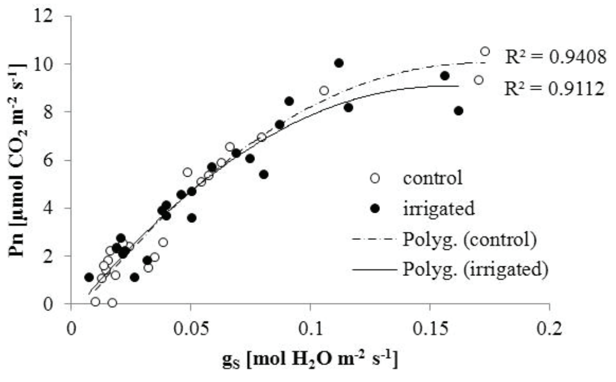

Fig. 2. CO_2 assimilation rate (P_N) as a function of stomatal conductance (g_S) in control (non-irrigated) and irrigated trees. Each data point represents a tree average value ($n = 23$ for each variant).

The average values of CO_2 assimilation rate of both groups of trees were similar at the end of June and the end of July (Fig. 3b), and no statistically significant differences were found.The differences in Ψ_S between groups were also small in these days (Fig 1). The mean values of P_N fluctuated from 4.09 to 6.86 µmol m^{-2} s^{-1} (irrigated) and from 4.19 to 7.49 µmol m^{-2} s^{-1} (control).

The maximum CO_2 assimilation rate of non-irrigated beech leaves were measured at the end of July, and the lowest mean values were recorded at the beginning of September (mean value was 1.61 µmol m^{-2} s^{-1}). P_N of irrigated beech leaves reached its peak at the same time as non-irrigated leaves, then at the end of August it decreased, but afterwards at the beginning of September it recovered to 5.28 µmol m^{-2} s^{-1}. The statistically significant differences in P_N between the groups of trees were confirmed for the third and the fourth measurements (when the differences in Ψ_S appeared). On these measurement days, the P_N values of irrigated individuals were approximately 1.9 or 3.3 times greater than the values of non-irrigated individuals.

Stomatal conductance is a parameter complexly expressing plant drought stress (Medrano et al. 2002). The course of stomatal conductance (g_S) was similar for both groups of trees except for the fourth measurement day (Fig. 3). The initial average values of g_S for both groups were between 0.039 and 0.049 mmol m^{-2} s^{-1}. Values then increased up to 0.087 mmol m^{-2} s^{-1} for the irrigated group and 0.1 mmol m^{-2} s^{-1} for the control, which was followed by decrease in the control group until the beginning of September, when the minimum value of 0.016 mmol m^{-2} s^{-1} was recorded. After the maximum at the end of July, stomatal conductance of the irrigated beech leaves decreased at the end of August, but consequently the g_S values recovered to 0.064 mmol m^{-2} s^{-1} at the beginning of September. Although the mean values of g_S of irrigated beeches were in almost all cases greater than the values of non-irrigated trees, statistically significant differences were revealed only on the last measuring day.

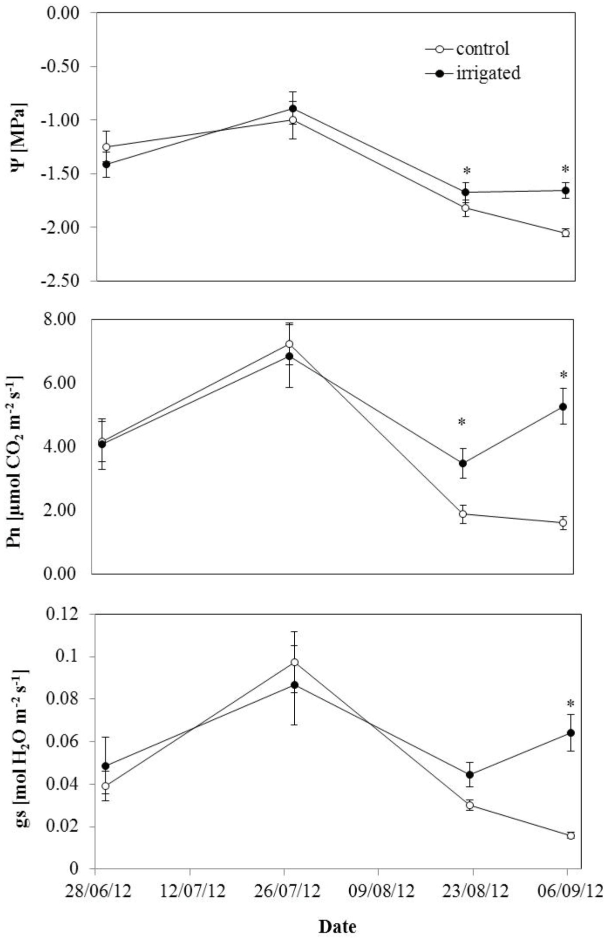

Fig. 3. Mean value (± standard error) of leaf water potential (Ψ_L), a), CO_2 assimilation rate (P_N), b) and stomatal conductance (g_S), c) of irrigated and non-irrigated trees; asterisks indicate significant differences ($P \leq 0.05$) between groups on the particular date (ANOVA, Duncan's test).

Both, P_N and g_S values were within the range found for mature European beech trees (Masarovičová & Štefančík 1990; Priwitzer 2001). On the last two dates, P_N and g_S were low in the control group, and Ψ_S reached the lowest values measurable by the used equipment (Fig. 1) indicating that water availability was low. Stomatal response of species with high g_S is more sensitive to environmental changes (Ewers et al. 2001). Raftoyannis & Radoglou (2002) compared the values of g_S between beech and sessile oak and showed that the values of beech were approximately half the values of oak. These results indicate that beech is less tolerant to drought than oak because of the lower reaction sensitivity of its stomata to drought. Species, and stands with high values of stomatal conductance at low *VPD* are also more sensitive to *VPD*, as

Table 2. Average maximal photochemical efficiency of photosystem II (F_v/F_m), ratio of photochemical efficiency to non-photochemical efficiency (F_v/F_0) and performance index (*PI*) of irrigated and control trees; asterisks indicate significant differences ($P \leq 0.05$) between groups on the particular date (ANOVA, Duncan's test).

Date	F_v/F_m		F_v/F_0		PI	
	control	irrigated	control	irrigated	control	irrigated
29/06/12	0.82	0.80*	4.49	4.21*	4.18	3.39*
27/07/12	0.81	0.80	4.31	4.06	4.19	3.73
22/08/12	0.83	0.83	4.79	4.79	5.38	5.78
06/09/12	0.82	0.81	4.50	4.37	5.65	5.05

required in order to maintain leaf water potential (Oren et al. 1999).

At the level of primary photosynthetic processes we did not observe lower values of the control individuals in comparison with the irrigated trees in any of the evaluated parameters (Table 2). Significantly more favourable values of fluorescence parameters of the control individuals were revealed only at the beginning of the experiment. This could result from the differences between the microclimatic conditions and the shift in pigments development during the growing season. Several authors observed the decrease in *PI* values with the advancing drought in different crops (Strasser et al. 2000; Živčák et al. 2008). In adult trees this reaction is probably the manifestation of acute stress and primary photochemical processes are more sensitive to high temperatures than to drought (Brestič & Živčák 2013). The gradual increase of the values during the growing season is the result of the annual dynamics of pigment content, and hence, it is the natural change in the efficiency of photochemical processes.

The long lasting drought period with minimal daily precipitation and high air temperatures caused the decrease of leaf water potential (Ψ_L) in the control trees (Fig. 3a). Gallé & Feller (2007) measured similar decrease in the values of Ψ_L due to drought in European beech trees. In the control group, higher values of the control group than in the irrigated group were measured only at the beginning of the season, before the first irrigation was applied. In spite of more favourable soil water conditions in the irrigated plot during the prevailing part of the growing season, Ψ_L of the irrigated group was slightly (but significantly) higher on the third and the fourth measuring date. The undermost values of Ψ_L were identified at the end of July for both variants with mean values –0.89 and –1.00 MPa. The plant water potential is one of the factors regulating the width of stomata openings and the values between –0.6 and –1.0 MPa start closing stomata in deciduous broadleaved trees (Larcher 1988). At the end of August, Ψ_L significantly decreased in both groups of beech trees and reached the average value of –1.67 in the irrigated and –1.82 MPa in the control group.

At the beginning of September, mean Ψ_L decreased in the non-irrigated beech trees to –2.08 MPa. Bréda et al. (1993) consider beech and oak under stress when Ψ_L falls below –2.00 MPa. From the values of Ψ_L it is evident that the course of Ψ_L is similar to stomatal conductance (g_S) and CO_2 assimilation rate (P_N). The leaf water potential decreased or increased on the same dates as P_N and g_S values. However, in September the values of g_S and P_N significantly increased in spite of the almost unchanged water potential of the irrigated trees (Fig. 3 a–c). This was probably due to lower values of *VPD*. Close relationship between Ψ_L and g_S was confirmed for the non-irrigated trees, but could not be confirmed for the irrigated trees (Fig. 4). It implies that Ψ_L is not the key factor in early stomata regulation. The response of stomata is more closely linked to air conditions and soil moisture content than to leaf water status (Yordanov et al. 2003). The decrease of Ψ_L seems to be the simple result of the reduced water availability rather than the reason of early stomatal closure (Kurjak et al. 2012).

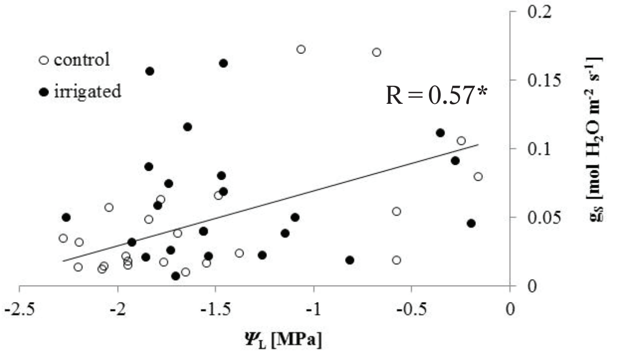

Fig. 4. Stomatal conductance (g_S) as a function of leaf water potential (Ψ_L) in the control (non-irrigated) and irrigated beech trees. Significant relationship for the control group is depicted. Each data point represents a tree average value ($n = 23$ for each variant).

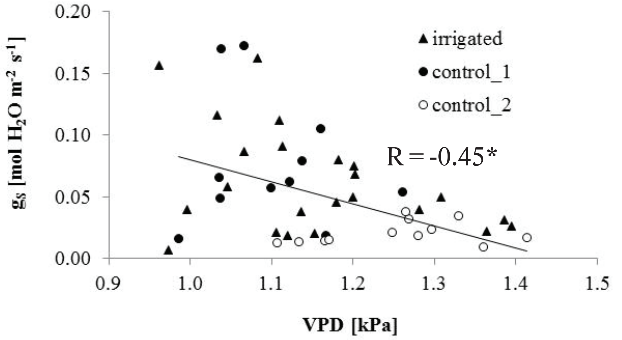

Fig. 5. Stomatal conductance (g_S) as a function of vapour pressure deficit (*VPD*) in the control (non-irrigated) and irrigated trees. Filled circles represent the data measured on the irrigated trees on the first and second measurement days before the great differences in soil water potential were observed, empty circles represent the data measured on the third and the fourth days. Significant relationship for the control group (all measurement days) is depicted. Each data point represents a tree average value ($n = 23$ for each variant).

Lendzion & Leuschner (2008) confirmed strong impact of VPD on beech seedlings growth. We revealed significant influence of VPD on gS only in the control group (Fig. 5). On the days when Ψ_S decreased, theof *VPD* values. Mesophyll resistivity for CO_2 diffusion may be another important factor limiting photosynthesis even when stomata are open (Flexas et al. 2012). Almost complete stomatal closure in both groups of trees was caused by the increase of *VPD* to 1.2 kPa.

Conclusion

The leaf water potential (Ψ_L), stomatal conductance (g_S) and consequently CO_2 assimilation rate (P_N) of European beech decreased with the increasing duration of drought. The P_N values of the irrigated individuals were greater than the values of the non-irrigated trees. Hence, drought-stressed trees may weaken and become less resistant to the impact of other negative factors. The assimilation rate was strongly controlled by the stomatal conductance, and we did not find any differences in primary photochemical processes between the groups during the drought. Stomatal conductance of the irrigated trees was strongly impacted by vapour pressure deficit and leaf water potential. Stomatal conductance in the control (non-irrigated) group of trees was affected by some other mechanisms (mesophyll resistance, abscisic acid production). Relatively low values of assimilation rate, even when stomata were fully opened, suggest that mesophyll conductance for CO_2 could be a significant factor influencing photosynthetic processes that could become an interesting scope for future studies.

Acknowledgments

This work was supported by the Slovak Research and Development Agency under the contract No. APVV-0111-10, APVV-0744-12 and APVV-0436-10.

References

Addington, R. N., Mitchell, R. J., Oren, R., Donovan, L. A., 2004: Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*. Tree Physiology 24:561–569.

Aranda, I., Gil, L., Pardos, J. A., 2000: Water relations and gas exchange in *Fagus sylvatica* L. *and Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. Trees: Structure and Function 14:344–352.

Baker, N. R., 2008: Chlorophyll fluorescence: a probe of photosynthesis in vivo Annual Review of Plant Biology 59:89–113.

Bréda, N., Cochard, H., Dreyer, E., Granier, A., 1993: Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. Canadian Journal of Forest Research 23:1136–1143.

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006: Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63:625–644.

Brestič, M., Živčák, M., 2013: PSII fluorescence techniques for measurement of drought and high temperature stress signal in crop plants: protocols and applications. In: Rout, G. R. & Das, A. B. (eds.): Molecular Stress Physiology of Plants. Springer India, p. 87–131.

Ciais, P. et al., 2005: Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533.

Cochard, H., Lemoine, D., Dreyer, E., 1999: The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. Plant, Cell & Environment 22:101–108.

Coll, L., Balandier, P., Picon-Cochard, C., 2004: Morphological and physiological responses of beech (*Fagus sylvatica*) seedlings to grass-induced belowground competition. Tree Physiology 24:45–54.

Cornic, G., 2000: Drought stress inhibits photosynthesis by decreasing stomatal aperture – not by affecting ATP synthesis. Trends in Plant Science 5:187–188.

Englisch, M., 2006: Die Rotbuche – ein Baumartenportrait. BFW--Praxis Information 12:3–6.

Ewers, B.E., Oren, R., Phillips, N., Strömgren, M., Linder, S., 2001: Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*. Tree Physiology 21:841–850.

FAO (2006) World reference base for soil resources. World soil resources reports 103. Food and Agriculture Organization of the United Nations, Rome.

Flexas, J. et al., 2012: Mesophyll diffusion conductance to CO_2: An unappreciated central player in photosynthesis. Plant Science 193:70–84.

Fotelli, M. A., Nahm, M., Radoglou, K., Rennenberg, H., Halyvopoulos, G., Matzarakis, A., 2009: Seasonal and interannual ecophysiological responses of beech (*Fagus sylvatica*) at its south-eastern distribution limit in Europe. Forest Ecology and Management 257:1157–116.

Fuhrer, J., Beniston, M., Fischlin, A., Frei, C., Goyette, S., Jasper, K. et al., 2006: Climate risks and their impact on agriculture and forests in Switzerland. Climatic Change 79:79–102.

Gallé, A., Feller, U., 2007: Changes of photosynthetic traits in beech saplings (*Fagus sylvatica*) under severe drought stress and during recovery. Physiologia Plantarum 131:412–421.

Geßler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2007: Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees 21:1–11.

Green Report of Ministry of Agriculture and Rural Development of the Slovak Republic, 2013: Report of the forestry sector in the Slovak Republic for the year 2012, 25 p.

Hlásny, T., Barcza, Z., Fabrika, M., Balázs, B., Churkina, G., Pajtík, J. et al., 2011: Climate change impacts on growth and carbon balance of forests in Central Europe. Climate Research 47:219–236.

Innes, J. L., 1992: Observation of the condition of beech (*Fagus sylvatica* L.) in Britain in 1990. Forestry 65:35–60.

Jamnická, G., Ditmarová, Ľ., Kurjak, D., Kmeť, J., Pšidová, E., Macková, M. et al., 2013: The soil hydrogel improved photosynthetic performance of beech seedlings treated under drought. Plant Soil and Environment 59:446–451.

Ježík, M., Blaženec, M., Střelcová, K., Ditmarová, Ľ., 2011: The impact of the 2003–2008 weather variability on intra-annual stem diameter changes of beech trees at a submontane site in central Slovakia. Dendrochronologia 29:227–235.

Kurjak, D., Střelcová, K., Ditmarová, Ľ., Priwitzer, T., Homolák, M., Pichler, V., 2012. Physiological response of irrigated and non-irrigated Norway spruce trees as a consequence of drought in field conditions. European Journal of Forest Research 131:1737–1746.

Landscape Atlas of the Slovak Republic, 2002: Bratislava, Ministry of the Environment of the Slovak Republic. Available at http://mapserver.geology.sk/Atlas_krajiny_sk/mapviewer.jsf.

Larcher, W., 1988: Fyziologická ekologie rostlin. Academia, Praha, 368 p.

Lendzion, J., Leuschner, C., 2008: Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. Forest Ecology and Management 256:648–655.

Masarovičová, E., Štefančík, L., 1990: Some ecophysiological features in sun and shade leaves of tall beech trees. Biologia Plantarum 32:374–387.

Mátyás, C., Berki, I., Czúcz, B., Gálos, B., Móricz, N., Rasztovits, E., 2010: Future of Beech in Southeast Europe from the Perspective of Evolutionary Ecology. Acta Silvatica et Lignaria Hungarica 6:91–110.

McDowell, N. G. et al., 2008: Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb? New Phytologist 178:719–739.

Medrano, H., Escalona, J. M., Bota, J., Gulias, J., Flexas, J., 2002: Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. Annals of Botany 89:895–905.

Oren, R., Sperry, J. S., Katul, G. G., Pataki, D. E., Ewers, B. E., Phillips, N. et al., 1999: Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant, Cell & Environment 22:1515–1526.

Pagan, J., Randuška, D., 1987: Atlas drevín 1. Bratislava, Obzor, 360 p.

Priwitzer, T., 2001: Vertical distribution of selected gas exchange parameters of leaves within the tall beech (*Fagus sylvatica* L.) crown profile. In: Minďáš, J. (ed.): Perspectives of the ecological research in mountain forest ecosystems. Zvolen, LVÚ Zvolen, p. 31–32.

Raftoyannis, Y., Radoglou, K., 2002: Physiological Responses of Beech and Sessile Oak in a Natural Mixed Stand During a Dry Summer. Annals of Botany 89:723–730.

Sitková, Z., Nalevanková, P., Střelcová, K., Fleischer, P. Jr., Ježík, M., Sitko, R. et al., 2014: How does soil water potential limit the seasonal dynamics of sap flow and circumference changes in European beech? Lesnícky časopis - Forestry Journal 60:19–30.

Strasser, R. J., Srivastava, A., Tsimilli-Michael, M., 2000: The fluorescence transient as a tool to characterize and screen photosynthetic samples. In: Yunus, M., Pathre, U., Mohanty, P. (eds.): Probing photosynthesis: mechanisms, regulation and adaptation. Taylor & Francis, London, p. 445–483.

Tognetti, R., Johnson, J.D., Michelozzi, M., 1995: The response of European beech (*Fagus sylvatica* L.) seedlings from two Italian populations to drought and recovery. Trees 9:348–354.

Urban, O., Anouš, D., Acosta, M., Czerny, R., Marková, I., Navratil, M. et al., 2007: Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. Global Change Biology 13:157–168.

Wilkinson, S., Davies, W. J., 2002: ABA-based chemical signalling: the co-ordination of responses to stress in plants. Plant, Cell & Environment 25:195–210.

Yordanov, I., Velikova, V., Tsonev, T., 2003: Plant responses to drought and stress tolerance. Bulgarian Journal of Plant Physiology special issue:187–206.

Živčák, M., Brestič, M., Olšovská, K., Slamka, P., 2008: Performance index as a sensitive indicator of water stress in *Triticum aestivum* L. L. Plant Soil and Environment 54:133–139.