



How does soil water potential limit the seasonal dynamics of sap flow and circumference changes in European beech?

Ako vodný potenciál pôdy limituje sezónnu dynamiku transpiračného prúdu a zmien obvodov kmeňa u buka lesného?

Zuzana Sitková^{1*}, Paulína Nalevanková², Katarína Střelcová², Peter Fleischer Jr.², Marek Ježík³, Roman Sitko², Pavel Pavlenda¹, Tomáš Hlásny^{1,4}

¹National Forest Centre - Forest Research Institute Zvolen, T. G. Masaryka 2175/22, SK – 960 92 Zvolen, Slovakia

²Technical University in Zvolen, Faculty of Forestry, T. G. Masaryka 24, SK – 960 53 Zvolen, Slovakia

³Institute of Forest Ecology Slovak Academy of Science, Štúrova 2, SK – 960 53 Zvolen, Slovakia

⁴Czech University of Life Sciences Prague, Kamýcká 129, CZ – 165 21 Praha 6 – Suchbátka, Czech Republic

Abstract

We focus on the analysis of sap flow and stem circumference changes in European beech (*Fagus sylvatica*, L.) in relation to available soil water and weather conditions during the growing seasons 2012 and 2013. The objective was to examine how soil water potential affects growth and transpiration of a mature beech stand situated at the lower distributional limit of beech in Slovakia. To be able to evaluate beech response to soil water shortage, we irrigated a group of 6 trees during the period of pronounced drought, while the control group of other 6 trees remained exposed to actual weather conditions. Mean air temperatures of both seasons were considerably above the long-term average and the temporal pattern of precipitation differed between the years. During the whole growing season 2012, beech samples transpired an average volume of 6.9 m³ of water in the control and 7.7 m³ in the irrigated group. A slightly higher average volume was found in the growing season 2013 under both treatments (7.7 m³ in control and 10.5 m³ in irrigated trees). In the drought period 2012, when the irrigation experiment was commenced, the sap flow in the control group was reduced by 30% as compared with the irrigated group. In 2013, a 38.1% difference in sap flow was observed between the groups. Sap flow in the non-irrigated trees decreased with reducing soil moisture, and ceased at soil water potential –0.6 MPa. In both treatments and years, we found significant correlations between hourly sap flow and investigated weather variables. A reduction in stem circumferences of the control trees, which was observed during stem shrinkage phase, was up to 19% in 2012 and 10% in 2013. We conclude that stem circumference shrinkage during the peak of soil drought was induced by the cessation in the sap flow process.

Keywords: *Fagus sylvatica*; transpiration; drought; stem shrinkage; irrigation treatment

Abstrakt

V práci sa zameriavame na analýzu transpiračného prúdu a zmien obvodov kmeňa buka lesného (*Fagus sylvatica* L.) vo vzťahu k disponibilnej pôdnej vode a meteorologickým podmienkam vo vegetačnom období 2012 a 2013. Cieľom bolo zistiť, ako vodný potenciál pôdy ovplyvňuje rast a transpiráciu bukového porastu na spodnej hranici výskytu buka na Slovensku. Počas periódy pôdneho sucha bola skupina 6 jedincov buka intenzívne zavlažovaná, zatiaľ čo kontrolná skupina 6 jedincov bola vystavená aktuálnym meteorologickým podmienkam. Vo vegetačnej sezóne oboch rokov boli zistené nadpriemerné mesačné teploty vzduchu. Časové rozloženie zrážok počas vegetačnej sezóny sa medzi rokmi líšilo. Vo vegetačnom období 2012, jedince buka transpirovali priemerne 6,9 m³ vody v kontrolnej skupine a 7,7 m³ v zavlažovanej skupine. V roku 2013 bol v oboch skupinách zistený vyšší objem transpiračného prúdu (priemerne 7,7 m³ v kontrolnej a 10,5 m³ v zavlažovanej skupine). V priebehu zavlažovacieho experimentu v období sucha 2012 bol transpiračný prúd jedincov kontrolnej skupiny v porovnaní so zavlažovanými jedincami buka nižší o 30 %. V roku 2013 bol medzi skupinami pozorovaný rozdiel 38,1 %. Vplyv pôdneho sucha na transpiráciu sa začal významne prejavovať pri hodnote vodného potenciálu pôdy –0,6 MPa. V oboch skupinách aj rokoch bol preukázaný štatisticky významný vzťah medzi hodinovými údajmi transpiračného prúdu a väčšinou skúmaných meteorologických charakteristík. Počas fázy zmršťovania kmeňov v období sucha, bol u jedincov kontrolnej skupiny pozorovaný 19 % pokles na obvode stromov v roku 2012 a 10 % v roku 2013. Na základe našich pozorovaní môžeme konštatovať, že kontrakcie obvodov kmeňov v období vrcholiaceho pôdneho sucha boli vyvolané útlmom v procese transpiračného prúdu.

Kľúčové slová: *Fagus sylvatica*; transpirácia; sucho; zmršťovanie obvodu kmeňa; zavlažovací experiment

*Corresponding author. Zuzana Sitková, e-mail: sitkova@nlcsk.org, phone: +421 45 531 41 58

1. Introduction

European beech (*Fagus sylvatica* L.) is a late-successional tree species of temperate forests nowadays covering an area of over 14 million ha of forest land in Europe (von Wühlisch 2008; Jump et al. 2012). In Slovakia, the share of beech has increased by 1.5% during the last ten years and currently covers 32.2% of the forest area (Green Report 2013).

During the recent two decades, an idea of converting secondary coniferous forests to more stable mixed forests has been promoted in forest policy and management in Europe (Dedrick et al. 2007). This particularly concerned even-aged spruce stands suffering from a range of biotic and abiotic disturbances (mainly air pollution, wind storms, bark beetles, fungal pathogens). Due to high vulnerability of Norway spruce forests, and potentially adverse effects of climate change on their sustainability, beech has been frequently considered as a suitable surrogate species for the conversion of some spruce forests (Dedrick et al. 2007; Lindner et al. 2010). On the other hand, various studies have pointed out the sensitivity of beech to prolonged droughts (Geßler et al. 2007; Granier et al. 2007). In a mixture with oak or spruce, European beech was found to be significantly more resistant to episodic drought stress than in monoculture (Pretzsch et al. 2012). Recently it was stated that extreme drought alters competitive dominance within as well as between beech and oak trees growing in mixed forests (Cavin et al. 2013). Hence enhancing the diversity of current beech forests seems a sound option for the adaptation of such forests to progressive drought (Hlásny et al. 2014).

Significant changes were predicted to occur in the xeric limit of beech distribution for the 21st century, and more than 20% of the current beech forests may appear in suboptimal climatic conditions (Stojanovic et al. 2013). Several reports from the southern regions of Europe suggested that vitality and persistence of beech can be threatened by drought, especially at lower altitudes and at southern range-edge of species distribution (Peñuelas et al. 2008; Jump et al. 2012; Silva et al. 2012). The long-term study from Switzerland concluded that beech trees at their dry distribution limit have exhibited better adaptation to extreme conditions, while at mesic sites significant seasonal shift in drought response was found, and the changes in the growth patterns of beech could be expected also under conditions with the higher available soil water capacity (Weber et al. 2013). For future silviculture, the marginal (eastern, continental) beech provenances may perform better under drought conditions (Rose et al. 2009). In Slovakia, production decline was projected to occur in ca. 20% of current beech forests, while mortality was projected to occur in 5% of beech forests close to species xeric distributional limit by the end of the century (Hlásny et al. 2011).

Physiological response of beech to drought has recently received considerable attention. Due to deep rooting system, beech forests have a considerable capacity to access deep soil water, and transfer it through transpiration process. Already at the beginning of the last century, it was reported that beech requires 75 litres for every 100 g of leaf substance (Pfeffer 1900). Thus, too frequent occurrence of reduction in transpiration induced by soil drought or high air temperatures may substantially affect water balance of the whole area.

A plant-water system has been investigated under both manipulated experiments on saplings (Rose et al. 2009; Kuster et al. 2012; Hartmann et al. 2013), and field-experiments conducted in natural conditions of forests (Leuzinger et al. 2005; Leuschner et al. 2001 etc.). As sap flow and transpiration are key indicators reflecting tree water status, these processes play a central role in plant drought research. In many recent studies, the physiological response of trees to various environmental variables (e.g. vapour pressure deficit, potential evapotranspiration, soil water potential), has been intensively examined (Gartner et al. 2009; Dalsgaard et al. 2011; MacKay et al. 2012; Kurjak et al. 2012; Klein et al. 2012; Štrélcová et al. 2013; Nadezhdina et al. 2014). A common finding is that sap flow and transpiration are strongly correlated, what enables one to infer tree transpiration from sap flow measurements (Schipka et al. 2005; Gartner et al.; Clausnitzer et al. 2011; Pokorný et al. 2012). In some studies, even the assumption that stand transpiration is equal to sap flow was successfully adopted (Urban et al. 2012). Hence, in this study we applied the same assumption. Soil water availability and weather conditions were repeatedly reported as crucial for tree growth and seasonal variation in stem circumferences (Dittmar & Elling 2007; Ježík et al. 2011; Vieira et al. 2013; Konôpka et al. 2014). Generally, development of climatic variables and water supply in early season (spring) has the major effect on stem diameter increment of forest trees (Michelot et al. 2012; Bošela et al. 2013).

Considering a central role of European beech in climate change adaptation in Central Europe, potential risks related to species drought-sensitivity even at mesic sites (Weber et al. 2013), and anticipated divergence of species responses to recent environmental changes (Mátyás et al. 2009), further research of beech physiological response to drought is needed.

This study addresses physiological response of mature beech trees to drought, and actual weather conditions. The main objectives are as follows: (i) to identify the periods of soil drought during the growing seasons 2012 and 2013 leading to substantial deterioration of beech physiological performance; (ii) to quantify sap flow rates and circumference changes in sample beech trees under contrasting soil moisture conditions (natural water stress versus water well-supplied trees); and (iii) to analyse the effect of weather variables on seasonal dynamics of sap flow and growth processes. On this basis, we strived to find out how soil water potential affects growth and transpiration of mature beech forests occurring at a lower altitudinal part of beech distribution in Slovakia.

2. Material and methods

2.1. Study site

The study site “Bienska” is located in the central part of Slovakia (48°36′43″N; 19°03′59″E) at an elevation 450 m a.s.l. (Fig. 1). The area is situated in the Kremnické vrchy Mts. and belongs to oak-beech altitudinal forest zone. The study forest is 65 years old and is dominated by European beech (*Fagus sylvatica*) with a minor admixture of sessile oak (*Quercus petraea*) and larch (*Larix decidua*), which however

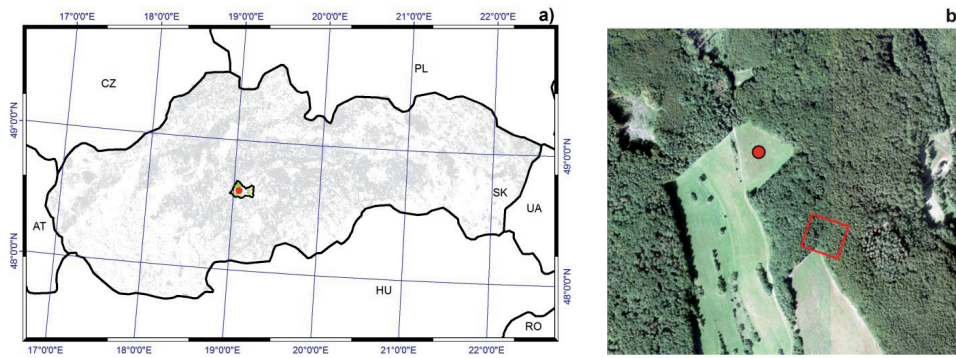


Fig. 1. Position of the study site in Central Slovakia (a). Position of the investigated stand (red square) and the local weather station (red dot) shown in the aerial photo of the area (b).

occur outside the experimental plot of 608 m². The site lies at the lower edge of beech distribution in Slovakia, where the effects of drought can be more pronounced. Total stand volume of beech is 282 m³ per hectare and relative stocking density of the forest stand is 0.85. The research plot is on the slight, east-facing slope. Based on the long-term data in the reference period 1961–1990, the mean annual temperature and annual precipitation totals is about 7.3 °C and 690 mm, respectively (Fig. 2).

Geological substrate of the study area is composed mainly of volcanic parent material (andesite and andesitic tuffs). According to WRB 2006, the soil at the research plot is classified as Haplic Cambisol (Humic, Eutric, Endoskeletal, Silty). The textural class of the fine earth fraction is qualified as silt loam in the topsoil (upper 30–35 cm) or loam in the subsoil. Only few coarse rock fragments are in the upper horizons, but abundant coarse gravel and stones are present in the subsoil (70–80% in C horizon). Higher content of coarse fragments is in the lower part of the research plot. The abundance of roots in the upper 35–40 cm of soil is relatively high. Only very few roots are present deeper in B/C and C horizons. The soil pH indicates slightly acidic soils. Measured values of exchangeable acidity are very low, base saturation is more than 80% in the whole soil profile. Cation exchange capacity values are between 15 and 25 cmol⁺ kg⁻¹. The content of soil organic carbon (SOC) is relatively high, which has a positive effect on soil structure and consistency. In A horizon the SOC content is about 5.5% and in the upper part of C horizon it is about 0.5–1.0%. The mean C/N ratio of 15.4 indicates good quality of soil organic matter. In terms of hydro-physical properties of the soil, the mean value of saturated hydraulic conductivity K_s was detected at $5.84 \times 10^{-5} \text{ cm s}^{-1}$ ($\pm 8.78 \times 10^{-4}$). K_s -values have a strong tendency to decrease with the depth at the site, and at a depth of 30 cm they substantially differ between the irrigated and the control part of the experimental plot.

2.2. Environmental data

The meteorological data were recorded during period May 2012–September 2013 using the automatic weather station (EMS Brno, Czech Republic) established at an open field close to the research stand. Air temperature (°C) and relative humidity (%) were measured every 5 minutes by EMS33

sensor located at a height of 2 m. Global radiation (W m^{-2}) was measured at 5-minute intervals by EMS11 sensor covered with Al071 radiation shield. Precipitation was recorded continuously at 1 meter above the ground, using the tipping bucket rain-gauge with resolution 0.2 mm per pulse and collecting area 320 cm² (Met One 370, USA). Measured data were stored as 20-minute averages in EdgeBox V12 datalogger (EMS Brno, CZ) powered by 12V solar-charged battery. Soil moisture expressed as soil water potential (Ψ , MPa) was measured under forest canopy using standard measuring-sets consisting of calibrated gypsum blocs (Delmhorst Inc., USA) and MicroLog SP3 datalogger (EMS Brno, CZ). Soil moisture measurements were conducted at three soil depths (15, 30 and 50 cm) and stored at 60-minute intervals.

To facilitate the investigation of physiological responses of stressed (control – “c”) and non-stressed (irrigated – “i”) trees, a watering system was built in the research plot. During dry periods detected on the base of the critical values of soil water potential, a group of 6 trees was irrigated. The 6 control sample trees were exposed to natural soil drought which occurred during the rainless period. Within 32 days in the summer drought period of 2012, we supplied 96 m³ of water. This volume represents ca. 820 mm of additional precipitation. During the drought period in 2013, we supplied 102 m³ of water. This corresponds to about 870 mm of additional precipitation supplied during 23 days.

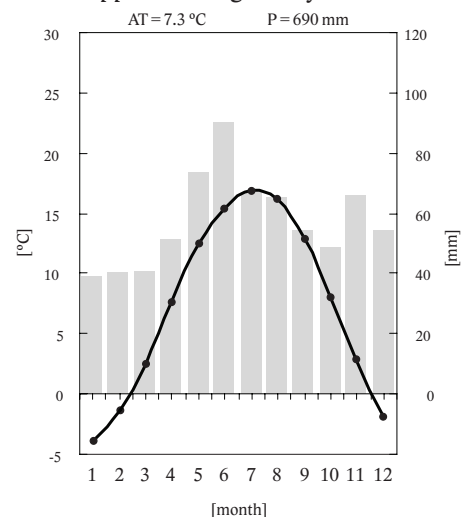


Fig. 2. Monthly mean annual air temperature AT (thick line) and precipitation totals P (bars) in the study site during the reference period 1961–1990.

2.3. Sap flow and potential evapotranspiration

The sap flow measurements were conducted on the trunks of 12 sample trees divided into two groups (6 irrigated; 6 control trees exposed to actual weather) using trunk heat balance technique (THB, Čermák et al. 2004). We used EMS51A sap flow system linked to the 16-channel datalogger RailBox V16 (EMS Brno, CZ). The temperature difference between the reference and the heated part of stem was set to the fixed value of 1K. The points of measurement were covered with reflective radiation shields. Sap flow values are measured in weight or volume units (kg or l) of water per certain period and per 1 cm of stem circumference. Subsequently, the totals of the transpired water were recalculated to an average tree on the base of the average stem circumference per group (m^3).

Potential evapotranspiration (PET, mm h^{-1}) at the research site was calculated using Penman equation (Penman 1948) (Equation 1).

$$PET = \frac{\Delta}{\Delta + \gamma} R_n + \frac{\gamma}{\Delta + \gamma} \frac{6.43 (1 + 0.536 u_2) D}{\lambda} \quad [1]$$

where, Δ is the slope of the saturation vapour pressure curve, R_n is the net radiation [W m^{-2}] estimated as 80% of global incoming solar radiation, and D [kPa] is the vapour pressure deficit ($e_s - e_a$) during the period, while e_a is the vapour pressure of free flowing air and e_s is the saturated vapour pressure at a given air temperature. The psychometric constant, γ , was set at 66 Pa K^{-1} . The latent heat of vaporization (λ) was set at 2.45 MJ kg^{-1} . The constant wind speed of 1.5 m s^{-1} at 2 m height was used (u_2) in calculation. Afterwards, hourly data were summed to daily totals of PET [mm day^{-1}].

2.4. Stem circumference measurements

Stem circumference changes (CIN, mm) were measured on the same sample trees at the height of 2.5 m using the automatic band dendrometers with embedded datalogger DRL26 and resolution $1 \mu\text{m}$ (EMS Brno, CZ). The data were stored in 20-minute intervals. The vital and representative beech trees within the experimental plot were chosen for the monitoring of stem circumferences.

2.5. Stand and tree characteristics

In November 2012, the stand characteristics of the study forest were measured using the Field Map technology (IFER Inc., Czech Republic). Measurements of tree heights, diameters at breast height and crown projections of 56 trees were taken over an experimental area of 608 m^2 (Fig. 3). An average diameter of the irrigated trees was 32.7 cm, ranging from 27.1–42.3 cm. Mean diameter of the control trees was 32.0 cm, with a range from 29.6–35.6 cm. Mean tree heights were 27.1 m (± 1.2) and 25.4 m (± 0.4) in the irrigated and the control group, respectively.

Leaf area index (LAI) of the beech experimental stand was assessed on the basis of the hemispherical photos taken in July 2012, i.e. on an approximate date of seasonal maximum LAI (LAI_{max}). Photo taking was carried out under favourable weather conditions (diffuse light) over an area

of the research stand in a regular square grid of 10×10 meters using camera Canon EOS 450D with “fish-eye” lens. The software *Hemisfer* (Schleppi et al. 2007) was used for interactive processing and analysis of hemispherical photographs. Based on the given approach, the average leaf area index of the study beech forest is 4.3 ranging from 3.8 to 4.9.

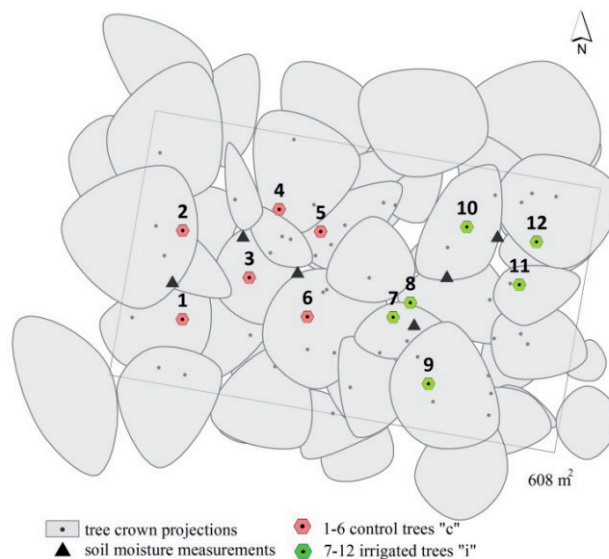


Fig. 3. Experimental design of the plot and positions of investigated trees.

2.6. Data analysis

All measured raw data, i.e. meteorological, soil moisture, sap flow and incremental data, were processed in Mini32 software (EMS Brno, CZ). The differences between the parameters of both variants (control and irrigated) during the drought periods were evaluated using the t-test. We used the analysis of variance (one way ANOVA) – Fisher’s LSD test – to identify the days with significant differences in daily sap flow values within the drought periods. The differences in transpiration between the years and the treatments during the drought periods were analysed by the two-way between-subjects ANOVA test. The interaction effect of both aspects (year as well as treatment) was analysed using one way ANOVA and Tukey HSD test. A correlation analysis was used to determine the dependency of sap flow and circumference changes on weather characteristics during the irrigation treatment. Statistical analyses were performed with STATISTICA Cz, v. 10 software (StatSoft, Inc., 2011).

The data were evaluated at three different intra-annual time scales: i/ over the whole season, ii/ during the drought periods, and iii/ during the days significantly differing in sap flow rates (SIG-days). In the case of the first time scale, the data were assessed for the whole growing season, from May to September. In the second case, we analysed the subset of the data covering two periods of 45 days, each selected from a drought period of one of the two analysed years, during which the irrigation was applied. Due to the actual weather situation, the beginning and the end of these periods differed between the investigated years. In the years 2012 and 2013, the data from 1st August to 14th September and from 12th July to 25th August, respectively, were used. In the third case,

only the data from the days detected as SIG-days, i.e. significantly different in sap flow rates were evaluated (27 individual SIG-days in 2012 and 11 SIG-days in the year of 2013). The abbreviations of all variables used in the paper are explained in Table 1.

3. Results

3.1. Environmental variables

The growing seasons of the years 2012 and 2013 were evidently warmer than the reference climate of the growing season for this site. Mean monthly air temperatures exceeded the long-term mean (1961–1990) by 2.6 °C to 3.4 °C, especially in July and August of both observed years (Fig. 4). From May to September 2012, we measured the rainfall total of 283 mm. During the same period in 2013, we recorded slightly higher precipitation total (407 mm) mainly due to exceptionally high rainfall in May (209% of precipitation normal). The July totals radically differed between the examined years. In 2012, rainfall reached 200% of normal value (136.3 mm), while precipitation total measured in July 2013 was deficient (29 mm, i.e. 43% of normal). The highest daily precipitation, 27.8 mm and 5.1 mm, were recorded on 29 July 2012 and 26 August 2013, respectively. The onset of the growing season in 2013 was affected by the prolonged cold weather, as the below-zero air temperatures were observed even within the first decade of April. Daily vapour pressure deficit ranged between 1.0–19.4 hPa and 0.1–20 hPa in the season of 2012 and 2013, respectively (Table 1). A total of potential evapotranspiration (PET) over the period May–September 2012 was 759 mm, and 706 mm in the year of 2013. Daily PET-maxima were observed on July 3, 2012 (8.9 mm) and July 24, 2013 (8.0 mm).

In terms of the development of soil moisture, the situation in 2013 was partially similar to that in 2012. The values of soil water potential (MPa) began to decline at the turn of June and July and a period of drought with risk values around –1.1 MPa persisted until the end of August (Fig. 5). In 2012, a period of significant soil drought started later, in early August and finished after an intensive rainfall in the first decade of September. The average values of soil water potential within the drought period of both years significantly varied between the control and the irrigated group of trees (Table 2). This provided an appropriate starting point and good precondition for further analysis of physiological data. In this paper we evaluate the data on sap flow and circumference changes. A more detailed analysis of further physiological parameters investigated in the experimental beech forest Bienska could be found in the separate contribution (Priwitzer et al. 2014).

3.2. Seasonal dynamics of sap flow

The evaluation of sap flow data over the **whole season** showed that during the growing season of 2012 the beech trees transpired an average volume of 69 l cm⁻¹ and 74 l cm⁻¹ in the control or irrigated group, respectively. A slightly higher sap flow volume was found in 2013 under both treatments (*SF_c* = 77 l cm⁻¹ and *SF_i* = 101 l cm⁻¹). The given values represent the mean amount of sap flow expressed in litres per 1 centimetre of stem circumference (an average per group). In 2012, the seasonal total volume of transpired water recalculated per mean tree of each individual group (based on average circumference of 6 sample trees) was 7.7 m³ in the irrigated and 6.9 m³ in the control variant. In the growing season 2013, we found the mean *SF*-volumes of 10.5 m³ and 7.7 m³ in the irrigated and the control group, respectively.

Table 1. Daily environmental and physiological variables measured at Bienska study site during the growing seasons 2012 and 2013. All variable abbreviations used in the paper are explained here.

Variable	Abbrev	Unit	Year 2012* / n = 137					Year 2013** / n = 153				
			x	min	max	SD	s _x %	x	min	max	SD	s _x %
Air temperature	AT	degree C	17.9	8.4	26.7	4.0	22	16.4	7.1	26.3	4.4	27
Relative air humidity	RH	%	68.9	46.1	94.1	11.8	17	73.6	46.3	99.1	12.5	17
Precipitation	P	mm day ⁻¹	1.9	0.0	27.8	4.5	235	2.7	0.0	51.0	6.7	253
Global radiation	GR	kWh m ⁻²	4.8	0.7	7.9	1.7	35	4.8	0.9	7.7	1.7	35
Vapour pressure deficit	D	hPa	7.9	1.0	19.4	4.0	50	6.5	0.1	20.1	4.5	69
Potential evapotranspiration	PET	mm day ⁻¹	4.9	0.7	8.6	1.8	37	4.6	0.8	7.9	1.9	41
Soil water potential "c"	Ψ _c	MPa	-0.4	-1.1	0.0	0.5	123	-0.3	-1.1	0.0	0.4	140
Soil water potential "i"	Ψ _i	MPa	-0.2	-0.7	0.0	0.2	106	-0.1	-0.9	0.0	0.2	124
Sap flow "c"	SF _c	l day ⁻¹ cm ⁻¹	0.5	0.0	1.2	0.4	69	0.5	0.0	1.2	0.3	60
Sap flow "i"	SF _i	l day ⁻¹ cm ⁻¹	0.5	0.0	1.1	0.3	53	0.7	0.0	1.6	0.4	61
Circumference changes "c"	CIN _c	μm	28.3	-110	469	78.7	279	38.7	-124	640	83.4	215
Circumference changes "i"	CIN _i	μm	31.0	-79	275	60.5	195	59.5	-86	339	79.2	133

* Year 2012 – from May 17 to September 30; **Year 2013 – from May 1 to September 30; "c" – control, non-irrigated group; "i" – irrigated group

Table 2. Testing of differences between mean values of sap flow (*SF*), soil water potential (*Ψ*) and circumference changes (*CIN*) under control and irrigated treatment during the drought periods 2012 and 2013. Significant results are bold-marked at $p < 0.05$.

variable	Unit	Drought period 2012* n = 45			Drought period 2013** n = 45		
		$x_c \pm sd_c$	$x_i \pm sd_i$	p-value	$x_c \pm sd_c$	$x_i \pm sd_i$	p-value
SF	[l day ⁻¹ cm ⁻¹]	0.44 ± 0.35	0.63 ± 0.26	0.005	0.59 ± 0.30	0.95 ± 0.39	0.000
CIN	[μm]	-21.5 ± 26.3	-2.17 ± 25.1	0.000	-1.80 ± 65.1	36.4 ± 66.0	0.007
Ψ	[MPa]	0.78 ± 0.41	0.43 ± 0.24	0.000	0.81 ± 0.35	0.33 ± 0.21	0.000

* Drought period in 2012 – from August 1 to September 14; **Drought period in 2013 – from July 12 to August 25; "c" – control, non-irrigated group; "i" – irrigated group

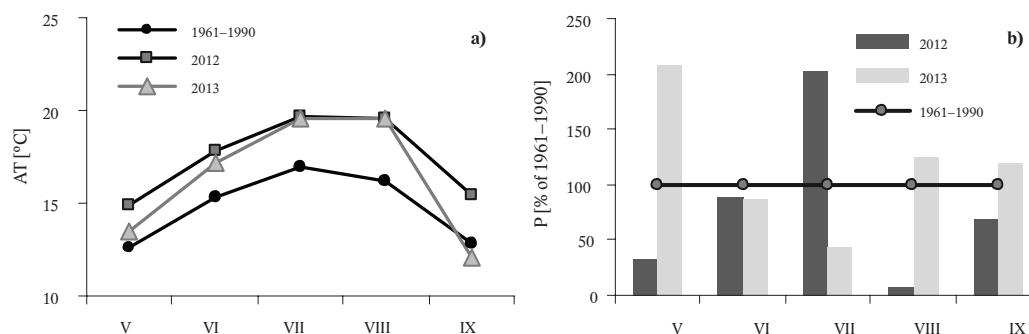


Fig. 4. Mean monthly air temperatures AT (a) and precipitation totals P as percentage of normal 1961–1990 (b) in the growing seasons 2012 and 2013.

The seasonal variability in sap flow expressed by coefficients of variation was comparable in both years and also within treatments (Table 1). The seasonal development of mean daily SF -values and major environmental variables assessed in this study is given in Figure 5.

The similar result to the whole-season period was also revealed from the **drought-period** data. The daily sap flow data during 45 drought days were compared between the years as well as between the two irrigation regimes using a two-way ANOVA test ($n = 1080$). The all tested effects were statistically significant. The volume of transpired water in both variants was higher in the year 2013 than in 2012 (Table 2, Fig. 6). In the drought period of 2012, the transpiration in the control variant was by 29.6% lower than the sap flow volume of the irrigated trees. In 2013, the difference between the groups was even slightly higher, 38.1%. Similarly, the interaction effect of both aspects (year as well as treatment) was found significant ($F = 11.1$, $p < 0.05$, partial $\eta^2 = 0.002$).

Over the vegetation seasons of 2012 and 2013, we identified 27, and 11 significant days (SIG-days), respectively, during which we found statistically significant differences in sap flow between the treatment groups (Fig. 6). The continuity of the SIG-days sequences was rarely aborted by small rainfall events; thereby the soil moisture conditions in the site were transiently enhanced. During the SIG-days we found significantly tight relationship between SF -values and almost all investigated weather variables (Table 3). We found the strongest dependency of transpiration (at $p < 0.05$) on vapour pressure deficit D and potential evapotranspiration PET , in both treatments and years. The positive and significant correlations were also observed with air temperatures AT and global radiation GR .

The regression curves demonstrating the relations of hourly SF_c and SF_i on D and GR during the SIG-days of

both seasons are given in Figure 7. In all cases, the steeper slope of regression lines is observed in SF_i as compared to that in SF_c . The reaction of irrigated trees is more dynamic and variable. However, the higher variance and dynamics may not be associated with a higher correlation coefficient (Table 3).

Likewise, we revealed statistically significant effect of soil water potential (Ψ) on SF under both regimes (Table 3). In 2012, the SF_c -values correlated with Ψ negatively, especially at depths of 30 cm ($r = -0.13$) and 50 cm ($r = -0.12$) in the control trees, and positively at a depth of 15 cm in the irrigated group of trees ($r = 0.12$). On the contrary, during SIG-days of 2013 we identified the positive and significant relationship between SF_i and Ψ only at a depth of 30 cm ($r = 0.15$). Weaker correlations between SF and Ψ in 2013 were probably caused by high daily rainfall recorded at the end of August (Fig. 5). We estimated that the control beech sample trees ceased their sap flow activity (SF_c) as soil water potential Ψ_c dropped approximately below -0.6 MPa. These responses of the drought-stressed trees occurring during both investigated seasons were observed especially at a soil depth of 30 cm.

Diurnal courses of global radiation GR , vapour pressure deficit D and sap flow SF in the irrigated and control beech trees are plotted in Figure 8. To capture the contrasting meteorological conditions in the both investigated years, we chose one clear and one cloudy day from each year. The greatest difference between the control and the irrigated group was recorded under the extreme values of D (4.1 kPa) on 9th August 2013 at about 14:00 PM. On that day, the reduction in sap flow of the control trees SF_c was significantly higher than during the selected clear day in 2012 (28th August), when D was visibly lower and reached the daily maximum of 2.3 kPa. During the cloudy days, the difference between SF_c

Table 3. Pearson's coefficients (r) of correlations between sap flow ($l\ h^{-1}\ cm^{-1}$) in irrigated (SF_i) and control (SF_c) beech trees and following variables: air temperature AT , precipitation P , global radiation GR , vapour pressure deficit D , potential evapotranspiration PET and soil water potential Ψ at three depths (-15 , -30 and -50 cm). Mean hourly SF -data during the days significantly different in sap flow rates (SIG-days) were used. Significant correlations are bold-highlighted at $p < 0.05$.

	AT	P	GR	D	PET	Ψ_{-15}	Ψ_{-30}	Ψ_{-50}
	[°C]	[mm]	[$W\ m^{-2}$]	[Pa]	[mm]	[bar]	[bar]	[bar]
Year 2012 / $n = 648$								
SF_c	0.76	-0.04	0.68	0.82	0.75	0.02	-0.13	-0.12
SF_i	0.79	-0.06	0.84	0.87	0.91	0.12	0.03	0.05
Year 2013 / $n = 264$								
SF_c	0.88	-0.01	0.72	0.92	0.80	0.09	-0.26	—
SF_i	0.82	-0.05	0.83	0.89	0.89	0.08	0.15	0.11

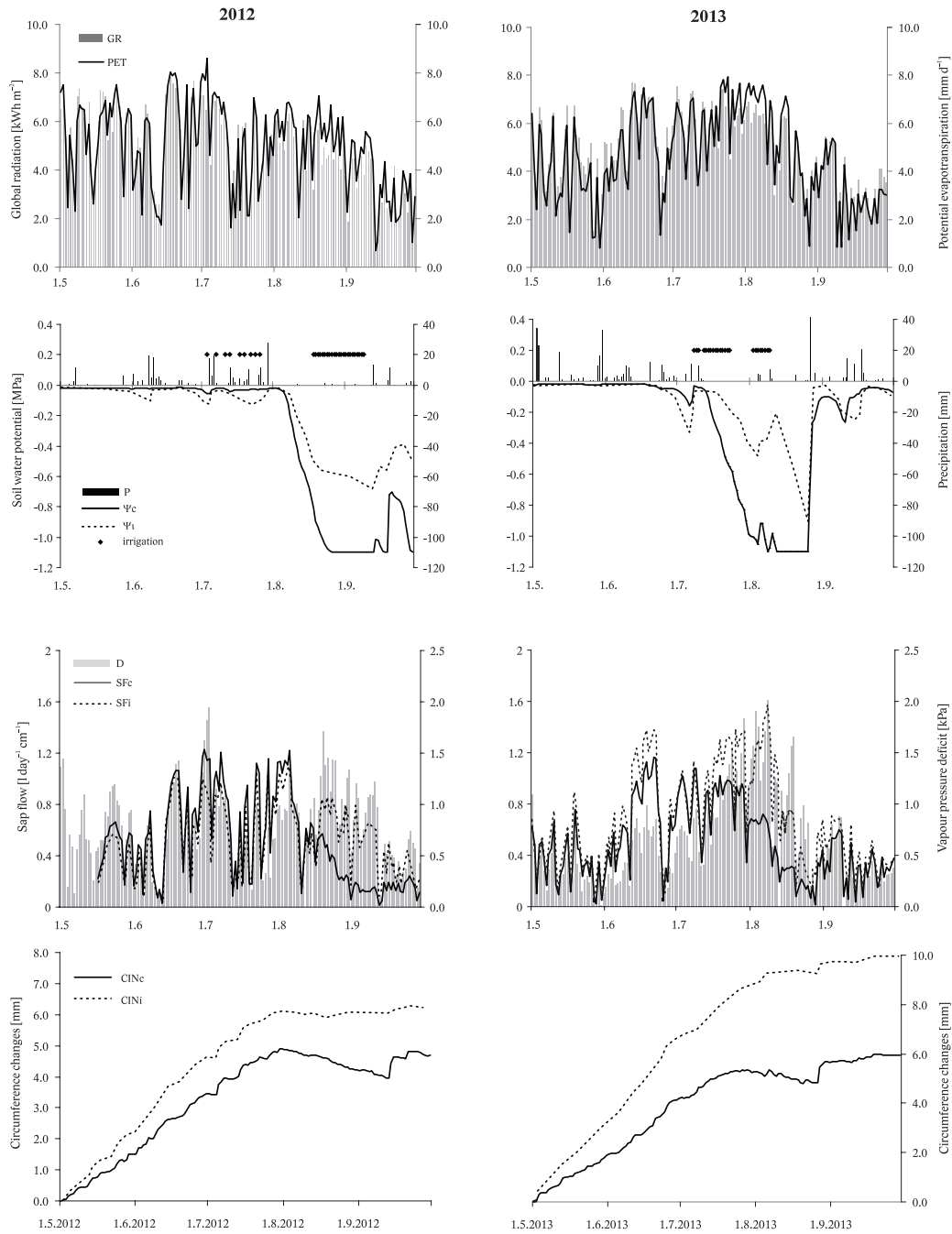


Fig. 5. Daily data of soil water potential Ψ (MPa), sap flow SF ($l\ day^{-1}\ cm^{-2}$), and seasonal circumference changes CIN (mm) in the irrigated (*i*) and control (*c*) group of beech samples. Besides, the irrigation days and relevant weather data (global radiation GR , precipitation P , potential evapotranspiration PET and vapour pressure deficit D) from May to September in 2012 and 2013 are plotted.

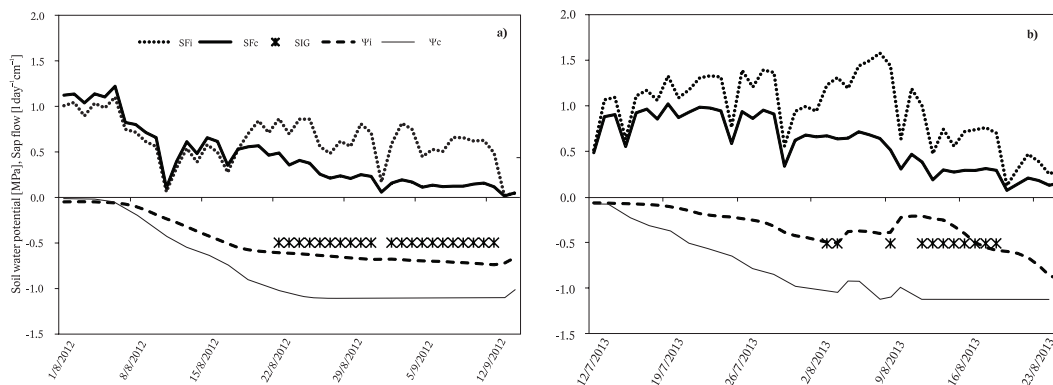


Fig. 6. Soil water potential Ψ (MPa), sap flow SF ($l\ day^{-1}\ cm^{-2}$) of the irrigated (*i*) and control (*c*) beech trees during the drought periods of 2012 (a) and 2013 (b). The days significantly different in sap flow rates within the drought periods (SIG) are indicated by asterisk.

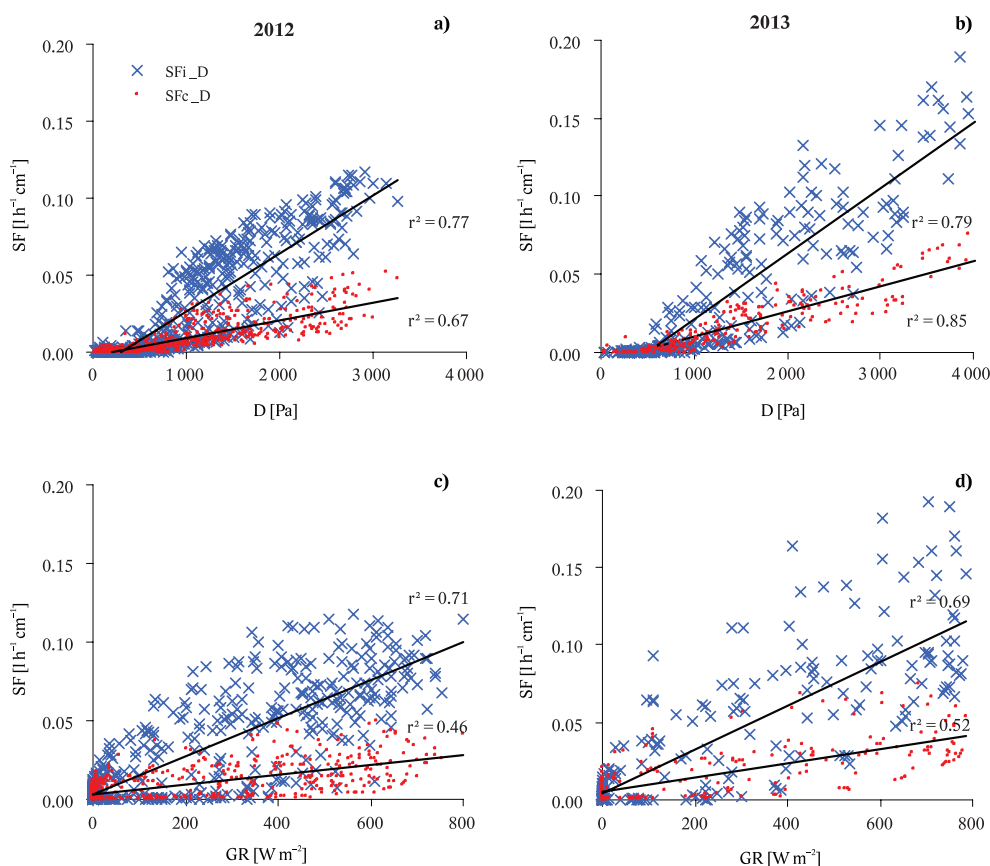


Fig. 7. Dependency of hourly sap flow values SF ($l\ h^{-1}\ cm^{-1}$) on vapour pressure deficit D (Pa) and global radiation GR ($W\ m^{-2}$) under different treatments (SFi and SFc) during the days significantly different in sap flow rates (SIG-days) in 2012 (a, c), and 2013 (b, d). All correlation coefficients are significant at $p < 0.05$.

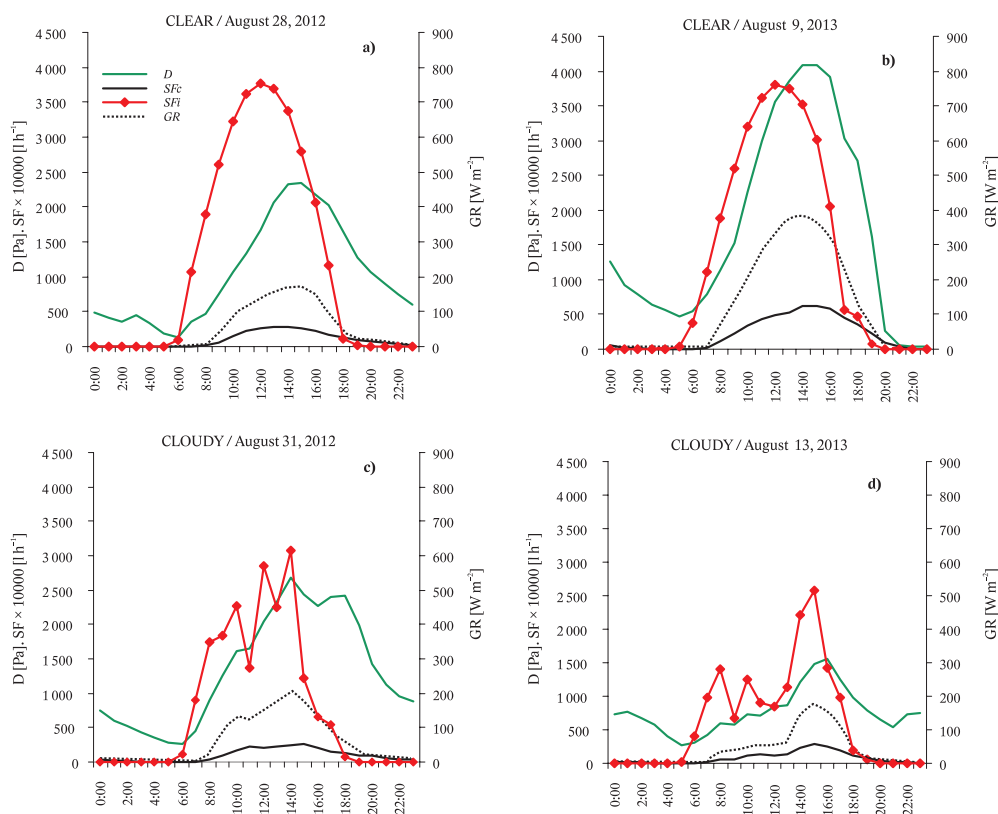


Fig. 8. Diurnal variation of sap flow ($l\ h^{-1}\ cm^{-1}$) in the irrigated (SFi) and control (SFc) trees with the daily course of global radiation GR and vapour pressure deficit D during the selected clear and cloudy days in both years 2012 (a, c) and 2013 (b, d). For easier comparison, the hourly sap flow values were multiplied by the factor 10 000.

and SFi was remarkable but not very large. The daily courses showed that during both years the measured beech trees were more sensitive to changes in D than GR .

3.3. Drought effect on stem circumference changes

Over the growing season 2012, the beech trees in the control group reached the average cumulative increment of about 4.7 mm (coefficient of variation, $CV=54\%$) compared to the irrigated trees which grew by 6.2 mm (42%). In 2013, the average seasonal cumulative increments of all beech trees within the control and the irrigated variants were 5.9 mm (59%) and 10 mm (31%), respectively. Thus, the higher tree-to-tree variability in seasonal cumulative increments was revealed in the control group within both monitored years (Table 1). The seasonal dynamics of stem circumference changes in the irrigated ($CINi$) and non-irrigated, control trees ($CINc$) were synchronized until the end of July in the both studied years (Fig. 5), with just slightly higher values in the irrigated group. The growth responses of the measured sample beech trees to environmental factors were very similar. In 2012, the end of the main period of stem circumference growth of both variants was recorded at the end of July, but in 2013 this was valid only for the control group. Afterwards, the control beech trees that were exposed to natural drought conditions, responded considerably to low precipitation and to the pronounced soil water shortage by shrinking of the stem circumferences.

An evaluation of the data observed during the drought periods showed that the daily circumference changes significantly differed between the treatments in both years (at $p < 0.05$) (Table 2). Nevertheless, the obvious reduction in the stem circumferences of the control sample trees $CINc$ recorded since the onset of shrinkage phase represented up to 19% in 2012 and only 10% in 2013 (Fig. 5). The shrinkage of beech stems in the control group was compensated by the expansion after enhanced moisture conditions and reduced soil water potential by rainfall. On the other hand, due to artificially added water, the irrigated trees showed the increase in stem circumferences also during the drought periods. It was more evident in 2013, when cumulative values of $CINi$ constantly rose until the end of the growing season; with the exception of the weak reduction occurring at the end of August. The presented fact is most probably caused by sufficient snow cover in the winter as well as abundant rainfall in May 2013, since it is known that soil water availability plays a key role in the creation of diameter increment. For instance, in “climate-growth” study (Michelot et al. 2012) beech was found as the most sensitive species to the climatic conditions of the current season and its growth was positively correlated with the precipitation from May to July.

The most detailed analysis of circumference data under drought conditions, when the soil water potential dropped to minimum (-1.1 MPa), showed statistically significant differences between the years as well as between the irrigation regimes. The data on maximum daily stem shrinkage (MDS) were analysed using two-way ANOVA ($n = 45$). The results showed that the effect of irrigation on stem circumference changes was significantly tighter in the year 2013 ($F=7.5$, $p <$

0.05 , $\eta^2=0.04$). The control sample trees showed only a small inter-annual difference in $CINc$, i.e. the growth response of the trees in this group was almost equal in both years. The inter-annual test confirmed higher seasonal increment in the year 2013 compared to that in 2012 (Tukey HSD test). However, no interaction effect (year & regime) on seasonal circumference increment of sample beech stems was found.

4. Discussion

Our results suggested that sap flow in mature beech trees was considerably reduced in the sample trees stressed by drought during the period of limited soil moisture. The control sample trees transpired significantly lower volume of water (by 38.1%), especially in the drought period of 2013, when compared to the sufficiently water-supplied trees. These findings comply with the results of other studies conducted at various species, such as Norway spruce (Clausnitzer et al. 2011; Střelcová et al. 2013), Douglas fir (Nadhezhhdina et al. 2014), Mediterranean Aleppo pine (Klein et al. 2012) or temperate White pine (MacKay et al. 2012). The apparent decrease of sap flow in birch and Norway spruce was observed with the proceeding drought in August 2003 in the southeastern Austria (Gartner et al. 2009).

Previous physiological investigations of European beech showed that relative maximum sap flow was reached at vapour pressure deficit of about 0.6 kPa, after which it progressively decreased as the drought advanced (Leuzinger et al. 2005). Our analysis of hourly sap flow data during the series of SIG-days in 2012 and 2013 indicated significant positive correlations between most of the investigated atmospheric variables (PET , D , GR , AT) and SF under both treatments (Table 3). The correlation coefficients (r) between SF and D ranged from 0.82 to 0.92 depending on the analysed year and treatment. The comparison of diurnal courses of SF -values under clear and cloudy sky conditions with hourly data of D and GR proved better accordance of SF with D than with GR (Fig. 8). Huang et al. (2009) suppose that during the soil water sufficiency, the transpiration is largely affected by vapour pressure deficit. In opposite cases, when the trees face the soil water shortage, which consequently result in stomatal closure, the transpiration might be affected by other variables rather than D . Similarly, global radiation and vapour pressure deficit were signed as major control drivers of stand transpiration, mainly at 75% of the spruce stand height (Pokorný et al. 2012). Vapour pressure deficit had also the primary control over the forest water loss of mature White pine studied in Southern Ontario, whereas soil moisture had an effect after that it dropped below 6.8% (MacKay et al. 2012). Relative transpiration (Ec/E_{cmax}) of a Norway spruce stand during the days with vapour pressure deficit above 1.45 kPa decreased linearly when soil water content dropped below 9.5vol%, but showed no significant relationship above this threshold (Clausnitzer et al. 2011). Leuzinger et al. (2005) stated that beech does not tolerate high vapour flux rates, therefore it down-regulates its transpiration by stomata closure at about $D = 10$ hPa. From the mesic species, *Fagus sylvatica* exhibited greater sensitivity to increasing vapour pressure deficit as a result of a greater loss of conductivity at high D in this ring-porous species as

compared to other species (Oren et al. 1999). The analysis of high resolution 10-min data of stomatal aperture in four tree species during four seasons proved distinctly different physiological responses to drought, leading to potential species-specific competitiveness (Zweifel et al. 2009).

The control sample beech trees subjected to the drought suffered from the soil water deficit particularly in the upper horizon. In the upper 15 cm of soil, SFC was not significantly influenced by the water shortage. The significant effect of soil water potential Ψ on SF was revealed at soil depths of 30 and 50 cm (Table 3). On the contrary, the artificial watering applied in the irrigated group of trees caused significant enhancement of Ψ_i at the upper 15 cm of soil and consequently had a positive effect on sap flow SFi . Based on the results of the two beech forest stands managed in a different way (even-aged managed versus uneven-aged natural) it was highlighted to consider the fact that the sap flow and water use are considerably affected by tree diameters and spatial heterogeneity (Dalsgaard et al. 2011). In our study, only weak correlation between SF and precipitation P was found, partly because the SIG-days were mainly concentrated into the dry periods when precipitation events were observed very rarely. However, at a regional scale the canopy transpiration of mature beech forests in a humid or semi-humid climate showed much weaker dependency on precipitation compared to the forest transpiration in semi-arid or arid climates (Schipka et al. 2005; Matyssek et al. 2009).

The beech trees investigated at Bienska study site showed significant response to descending soil water potential also in stem circumference changes. Within the shrinkage phase, the obvious reduction of $CINc$ was observed in the control samples comparing to that in the irrigation variant ($CINi$) (19% in 2012 versus 10% in 2013). The slightly lower decrease of $CINc$ in 2013 could be reasoned by the occurrence of small precipitation during the dry period and the ongoing irrigation treatment in the middle of August (Fig. 5). Since the rainfall events during the drought usually induce rapid restoration of vapour fluxes (Granier et al. 2007), it can consequently lead to fluctuations in stem circumferences. Due to stem re-hydration after significant precipitation we observed rapid expansion in the control beech sample trees, subsequently leading to slight restoration of physiological activity. These breakpoints were caused by rainfall events and finally finished the drought periods in the time lag of about 18 days between the investigated years. MacKay et al. (2012) found a 17% decrease in the growth of pine in the drought plot as compared to the reference plot, during the growing season 2009. The research of daily variations in stem radius of maritime pine showed 10 times higher amplitude of contraction and recovery during the summer shrinking period in comparison to other periods (Vieira et al. 2013). The monitoring of the continuous changes in stem radius offers possibilities for mutual analysis among various environmental variables. For instance, this kind of data was efficiently used for linking stem growth and net ecosystem productivity (NEP) in sub-alpine Norway spruce forests. A remarkably close and positive relationship was found between NEP and stem radius changes at monthly and annual scales (Zweifel et al. 2010). As the changes in stem water potential could be immediately sensed by digital dendrometers, for example as a result of the spring bud break (Urban et al. 2013), in future research we

are able to link these high resolution physiological measurements with eventual phenological data.

5. Conclusion

Given the ecological and economic importance of European beech, the scientific community is faced with the questions on anticipated impacts of climate change on the future of Central European beech forests. Moreover, negative effects of the recent environmental changes on forest ecosystems are amplified in many regions by various collateral stressors such as acidification, nitrogen deposition, ozone concentrations, heavy metals load or nutrient leaching. Thus, diverse studies from various areas of Europe are needed to collect a critical mass of information about the drought-sensitivity of beech forests facilitating their sustainable management under the changing environment.

Since the air temperature and warm-season vapour pressure deficit were recently found to be the main potent drivers of drought stress with negative effects on tree mortality, forest productivity (Williams et al. 2013) and carbon balance of whole-plants (Zhao et al. 2013), there is a growing need of complex ecophysiological research based on field and laboratory experiments. The meteorological conditions which occurred during the experiment presented in the current study provided unique basis for such research. We revealed a significant response of sap flow in mature beech trees to irrigation treatment during the dry periods in two investigated years. The results suggested that there is a strong interaction between the soil and atmospheric drought, and the growth performance and water status of beech trees subjected to prolonged low soil water potential. On the basis of our observations we can clearly elucidate that stem circumference shrinkage during the peak period of soil drought was induced by the cessation in the transpiration process. Thus, we can conclude that decreasing soil water availability significantly limited tree growth as well as sap flow rates in the investigated beech stand.

Acknowledgement

The study was supported by the Slovak Research and Development Agency under the contracts No. APVV-0111-10, APVV-0268-10 and APVV-0436-10. This work is partially the result of the project implementation Demonstration object on the transformation of declining spruce forests into ecologically more stable multifunctional ecosystems, ITMS 26220220026, supported by the Research & Development Operational Program funded by the ERDF (20%).

References

- Bošela, M., Pajtk, J., Konôpka, B., Šebeň, V., Vida, T., 2013: Modeling effects of weather condition on seasonal dynamics of the stem circumference increment in a mixed stand of Norway spruce and European beech. *Lesnický časopis - Forestry Journal* 59:180–188.
- Cavin, L., Mountford, E. P., Peterken, G. F., Jump, A. S., 2013: Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology* 27:1424–1435.

- Čermák, J., Kučera, J., Nadezhdina, N., 2004: Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees* 18:529–546.
- Clausnitzer, F., Köstner, B., Schwärzel, K., Bernhofer, C., 2011: Relationships between canopy transpiration, atmospheric conditions and soil water availability—Analyses of long-term sap-flow measurements in an old Norway spruce forest at the Ore Mountains/Germany. *Agricultural and Forest Meteorology* 151:1023–1034.
- Dalsgaard, L., Mikkelsen, T. N., Bastrup-Birk, A., 2011: Sap flow for beech (*Fagus sylvatica* L.) in a natural and a managed forest—effect of spatial heterogeneity. *Journal of Plant Ecology* 4:23–35.
- Dedrick, S., Spiecker, H., Orazio, C., Tomé, M., Martínez, I. (eds.), 2007: Plantation or Conversion – The Debate! Ideas presented and discussed at a joint EFI Project-Centre conference held 21–23 May 2006 in Freiburg, Germany. Discussion Paper, 13: 98 p.
- Dittmar, C., Elling, W., 2007: Dendroecological investigation of the vitality of Common Beech (*Fagus sylvatica* L.) in mixed mountain forests of the Northern Alps (South Bavaria). *Dendrochronologia* 25:37–56.
- Gartner, K., Nadezhdina, N., Englisch, M., Čermák, J., Leitgeb, E., 2009: Sap flow of birch and Norway spruce during the European heat and drought in summer 2003. *Forest Ecology and Management* 258:590–599.
- Gefler, A., Keitel, C., Kreuzwieser, J., Matyssek, R., Seiler, W., Rennenberg, H., 2006: Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* 21:1–11.
- Granier, A., Reichstein, M., Bréda, N., Janssens, I. A., Falge, E., Ciais, P. et al., 2007: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology* 143:123–145.
- 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.
- Hartmann, H., Ziegler, W., Kolle, O., Trumbore, S., 2013: Thirst beats hunger – declining hydration during drought prevents carbon starvation in Norway spruce saplings. *New Phytologist* 200:340–349.
- 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.
- Hlásny, T., Mátyás, C., Seidl, R., Kulla, L., Merganičová, K., Trombik, J. et al., 2014: Climate change increases the drought risk in Central European forests: What are the options for adaptation? *Lesnický časopis - Forestry Journal* 60:5–18.
- Huang, Y., Zhao, P., Zhang, Z., Li, X., He, Ch., Zhang, R., 2008: Transpiration of *Cyclobalanopsis glauca* (syn. *Quercus glauca*) stand measured by sap-flow method in a karst rocky terrain during dry season. *Ecological Research* 24:791–801.
- Ježík, M., Blaženc, M., Střelcová, K., Ditmarová, L., 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.
- Jump, A., Rico, L., Coll, M., Peñuelas, J., 2012: Wide variation in spatial genetic structure between natural populations of the European beech (*Fagus sylvatica*) and its implications for SGS comparability. *Heredity* 108:633–639.
- Klein, T., Rotenberg, E., Cohen-Hilaleh, E., Raz-Yaseef, N., Tatarinov, F., Preisler, Y. et al., 2012: Quantifying transpirable soil water and its relations to tree water use dynamics in a water-limited pine forest. *Ecohydrology*, Available at: DOI:10.1002/eco.1360.
- Konôpka, B., Pajtík, J., Bošela, M., Hlásny, T., Sitková, Z., 2014: Inter- and intra- annual dynamics of height increment in young beech and spruce stands in relation to tree size and weather conditions. *Lesnický časopis - Forestry Journal* 60:51–59.
- Kurjak, D., Střelcová, K., Ditmarová, L., Priwitz, T., Kmet', J., 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.
- Kuster, T. M., Arend, M., Bleuler, P., Günthardt-Goerg, M. S., Schulin, R., 2013: Water regime and growth of young oak stands subjected to air-warming and drought on two different forest soils in a model ecosystem experiment. *Plant Biology (Stuttg)* 15 (Suppl 1):138–147.
- Leuschner, C., Backes, K., Hertel, D., Schipka, F., 2001: Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management* 149:33–46.
- Leuzinger, S., Zotz, G., Asshoff, R., Korner, CH., 2005: Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiology* 25:641–650.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J. et al., 2010: Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management* 259:698–709.
- MacKay, S. L., Arain, M. A., Khomik, M., Brodeur, J. J., Schumacher, J., Hartmann, H. et al., 2012: The impact of induced drought on transpiration and growth in a temperate pine plantation forest. *Hydrological Processes* 26:1779–1791.
- Mátyás, C., Božic, G., Gömöry, D., Ivankovic, M., Rasztovits, E., 2009: Juvenile growth response of European Beech (*Fagus sylvatica* L.) to sudden change of climatic environment in SE European trials. *iForests, Florence* 2:213–220.
- Matyssek, R., Wieser, G., Patzner, K., Blaschke, H., Häberle, K.H., 2009: Transpiration of forest trees and stands at different altitude: consistencies rather than contrasts? *European Journal of Forest Research* 128:579–596.
- Michelot, A., Bréda, N., Damesin, C., Dufrêne, E., 2012: Differing growth responses to climatic variations and soil water deficits of *Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris* in a temperate forest. *Forest Ecology and Management* 265:161–171.
- Nadezhdina, N., Urban, J., Čermák, J., Nadezhdin, V., Kantor, P., 2014: Comparative study of long-term water uptake of Norway spruce and Douglas-fir in Moravian upland. *Journal of Hydrology and Hydromechanics* 62:1–6.
- 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 and Environment* 22:1515–1526.
- Penman, H. L., 1948: Natural evaporation from open water, bare soil, and grass. *Proceedings of the Royal Society London Ser A* 193:120–146.
- Peñuelas, J., Hunt, J. M., Ogaya, R., Jump, A. S., 2008: Twentieth century changes of tree-ring $\delta^{13}C$ at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology* 14:1076–1088.
- Pfeffer, W., 1900: *The Physiology of Plants, a Treatise upon the Metabolism and Sources of Energy in Plants*. Translated by A. J. Ewart. Vol. I. 632 p. Oxford, 1900. Vol. II, 296 p. Oxford, 1906. Vol. III. 451 p. Oxford, 1906.
- Pokorný, R., Slípková, R., Havránková, K., Pavelka, M., 2012: Ecosystem water use efficiency of Norway spruce monoculture from eddy-covariance and ecophysiological measurements. *Acta Horticulturae (ISHS)* 951:301–307.

- Pretzsch, H., Schütze, G., Uhl, E., 2013: Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biology (Stuttg)* 15:483–495.
- Priwitzer, T., Kurjak, D., Kmeť, J., Sitková, Z., Leštianska, A., 2014: Photosynthetic response of European beech to atmospheric and soil drought. *Lesnícky časopis - Forestry Journal* 60:31–37.
- Rose, L., Leuschner, C., Köckemann, B., Buschmann, H., 2009: Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research* 128:335–343.
- Schipka, F., Heimann, J., Leuschner, C., 2005: Regional variation in canopy transpiration of Central European beech forests. *Oecologia* 143:260–270.
- Schleppi, P., Conedera, M., Sedivy, I., Thimonier, A., 2007: Correcting non-linearity and slope effects in the estimation of the leaf area index of forests from hemispherical photographs. *Agricultural and Forest Meteorology* 144:236–242.
- Silva, D. E., Rezende Mazzella, P., Legay, M., Corcket, E., Dupouey, J. L., 2012: Does natural regeneration determine the limit of European beech distribution under climatic stress? *Forest Ecology and Management* 266:263–272.
- StatSoft, Inc., 2011: STATISTICA (data analysis software system), version 10. Available at: <www.statsoft.com>.
- Stojanović, D. B., Kržič, A., Matović, B., Orlović, S., Duputic, A., Djurdjević, V. et al., 2013: Prediction of the European beech (*Fagus sylvatica* L.) Xeric limit using a regional climate model: An example from southeast Europe. *Agricultural and Forest Meteorology* 176:94–103.
- Střelcová, K., Kurjak, D., Leštianska, A., Kovalčíková, D., Ditmarová, L., Škvarenina, J. et al., 2013: Differences in transpiration of Norway spruce drought stressed trees and trees well supplied with water. *Biologia* 68:1118–1122.
- Urban, J., Bednářová, E., Plichta, R., Kučera, J., 2013: Linking phenological data to ecophysiology of European beech. *Acta Horticulturae (ISHS)* 991:293–299.
- Urban, J., Gebauer, R., Nadezhdina, N., Čermák, J., 2012: Transpiration and stomatal conductance of mistletoe (*Loranthus europaeus*) and its host plant, downy oak (*Quercus pubescens*). *Biologia* 67:917–926.
- Vieira, J., Rossi, S., Campelo, F., Freitas, H., Nabais, C., 2013: Seasonal and daily cycles of stem radial variation of *Pinus pinaster* in a drought-prone environment. *Agricultural and Forest Meteorology* 180:173–181.
- von Wühlisch, G., 2008: EUFORGEN Technical Guidelines for genetic conservation and use for European beech (*Fagus sylvatica*). Bioersivity International, Rome, Italy. 6 p.
- Weber, P., Bugmann, H., Pluess, A. R., Walthert, L., Rigling, A., 2013: Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees* 27:171–181.
- Williams, A. P., Allen, C. D., MacAlady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M. et al., 2013: Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3:292–297.
- Zhao, J., Hartmann, H., Trumbore, S. E., Ziegler, W., Zhang, Y., 2013: High temperature causes negative whole-plant carbon balance under mild drought. *New Phytologist* 200:330–339.
- Zweifel, R., Eugster, W., Etzold, S., Dobbertin, M., Buchmann, N., Häsler, R., 2010: Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps. *The New Phytologist* 187:819–830.
- Zweifel, R., Rigling, A., Dobbertin, M., 2009: Species-specific stomatal response of trees to drought – a link to vegetation dynamics? *Journal of Vegetation Science* 20:442–454.