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Differences in transpiration of Norway spruce drought stressed trees and trees well supplied with water**

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Abstract: The paper focuses on the evaluation of transpiration as a physiological process, which is very sensitive to drought stress. Reactions of 25-year-old Norway spruce (*Picea abies* (L.) Karst.) trees to drought were examined during 2009 summer. Sap flow rate (SF), meteorological and soil characteristics were measured continually. Vapour pressure deficit of the air (VPD) and cumulative transpiration deficit (KTD) was calculated. During the second half of the vegetation period, the decrease in soil water content was observed and irrigation was applied to a group of spruce trees, while the second group was treated under natural soil drought. On the days, when the differences in transpiration between irrigated (IR) and non-irrigated (NIR) trees were significant (21 days), transpiration of NIR trees was only 23% of the transpiration of IR trees. We found significant differences in transpiration when the soil water content (SWC) of NIR variant at a depth of 5–15 cm ranged from 10.4 to 13.7%. Under both regimes of water availability, daily transpiration significantly responded to atmospheric conditions. However, the influence of all assessed meteorological parameters on SF of NIR trees was significantly lower than on IR tree. The dependency of transpiration on evaporative demands of atmosphere decreased with the decreasing soil moisture. Cumulative transpiration deficit of the stand during the entire evaluated period was 50.9 mm. The difference between the transpiration of the mean NIR tree and of the mean IR tree was 278.8 L over the assessed period of 47 days (5.9 L per day). The transpiration of NIR trees was 40.3% from the transpiration of IR trees during this period.

Key words: *Picea abies*; drought stress; soil moisture; sap flow; transpiration deficit

Introduction

Nowadays, increasing attention has been paid to monitoring of drought incidence and intensity, and its impact on forest ecosystems. Under the conditions of humid temperate zone, intense drought episodes should not be considered as isolated extreme events, rather as events, which in near future can be repeated with increasing frequency. The attention should be paid to the impact of these changes on the hydrological conditions of forests, because severe and repeated droughts are currently considered as one of the main factors contributing to forest dieback in Europe (Bredemeier et al. 2011). Under the climatic conditions of Central Europe, tree species do not have sufficiently efficient defence mechanisms or strategies to survive severe drought periods without negative impact on their physiological processes and subsequently on their growth, production and the overall vitality. A number of authors point out that drought stress and high summer air temperatures have a direct influence on physiological processes, phenology and ultimately also on tree species distribution and occurrence (Beniston & Innes 1998; Kurjak et al. 2012). In Central Europe, Norway spruce was frequently planted outside the areas of its natural occurrence and its ecological optimum. In Slovakia, there are currently 250,000 ha of unnatural spruce stands, which is approximately one half of the total area of spruce forests (Kulla & Sitková 2012).

Transpiration and sap flow is an important physiological process that can reflect water conditions of the tree and reacts to drought stress very sensitively. In general, the relationship between SF and transpiration is linear, and can be used for the calculation of tree transpiration (Clausnitzer et al. 2011). Sap flow and transpiration are closely correlated not only to meteorological factors, such as vapour pressure deficit and potential evapotranspiration (Dragoni et al. 2009; Köhler et al. 2010), but also to soil water content and physiological parameters (Nadezhdina at al. 2010; Dalsgaard et al. 2011; Klein at al. 2012). Availability of soil water to plants is a significant factor affecting transpi-

*Corresponding author, **Special Section on Biohydrology, guest-editors Ľubomír Lichner & Kálmán Rajkai ration process, because water supply may be reduced and problematic under the conditions of climate drying transpiration (Homolák et al. 2009; Hríbik et al. 2012; Lichner et al. 2012).

The goal of the work is to assess the changes in spruce transpiration due to irrigation; to determine at which soil water content the transpiration of trees under drought stress is significantly different from the transpiration of irrigated trees; to analyse the relationships between transpiration and atmospheric factors; and to determine the cumulative transpiration deficit.

Material and methods

The experimental site Hriňová is situated in central Slovakia (Central Europe 48°34′24″ N, 19°31′22″ E), at an elevation of about 655 m a.s.l. Mean annual temperature is 6.5 °C, and mean annual precipitation is 740 mm. The forest is 25 years old and is dominated by Norway spruce (*Picea abies* [L.] Karst). The site is situated outside the natural occurrence of spruce forests. In summer during the period of soil water deficit, irrigation was applied to a group of 5 spruce trees. From July 16th till August 30th, 23 m^3 of water was distributed to the irrigated group (IR). Water was slowly outflowing from the containers through a dripping system to minimize surface runoff. The second group of 6 non-irrigated (NIR) trees was treated under natural soil drought. Stem circumference of the mean sample tree was 55.2 cm.

Air temperature, relative humidity, global radiation and precipitation were measured at 20-min intervals (datalogger Minikin RTH, EMS Brno, CZ, MetOne 370, USA) outside the forest stand at a nearby open space. SWC (reflectometric principle, TDR) was measured continually inside the forest stand (Campbell, Campbell Scientific, USA), stored at 60-min intervals and calibrated using the values determined gravimetrically every 2 weeks at depths of 5–15 cm. Data were processed using Mini32 software (EMS Brno, CZ).

The sap flow of spruce trees was estimated by direct non-destructive and continuous measurements using tree-trunk heat balance method (THB, Čermák & Kučera 1981) with internal heating of xylem tissues and temperature sensing (Sap Flow EMS 51, EMS Brno, Czech Republic). Data were stored at 20-min intervals. Sap flow rates of particular trees were estimated by applying the tree-trunk heat balance method. Needle water potential was measured before

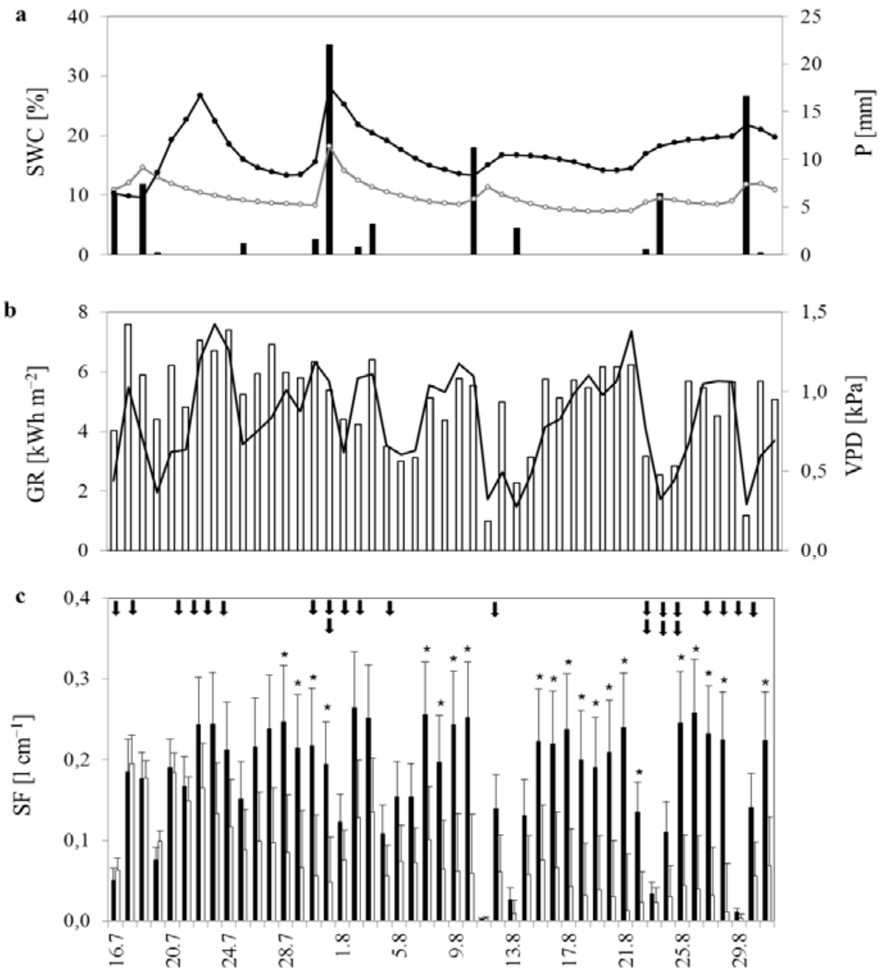

Fig. 1. Volumetric soil water content of the irrigated (filled circle, black line) and non-irrigated (open circle, grey line) plot at a soil depth of 5–15 cm (SWC) and daily precipitation (bars, P) (a), global radiation (GR, bars) and vapour pressure deficit (VPD, line) (b), mean sap flow rate (SF) ± standard error in irrigated (black bars) and non-irrigated (white bars) trees (c). Each arrow indicates 1 m^3 of water used for irrigation. Asterisks indicate significant differences ($P \leq 0.05$) between groups (ANOVA, Duncan's test).

first irrigation and three times during evaluated period with PSY-PRO instrument (Wescor, USA) based on psychrometric principle.

KTD was calculated as a sum of the differences between the transpiration of spruce trees well supplied with water and the trees treated under natural soil drought. KTD was converted to per hectare values [mm] and reduced with stocking.

The differences between the groups were tested with ANOVA. Means were compared using Duncan's multiple-range tests, at a significance level $P < 0.05$. ANOVA and regression analyses were performed employing Statistica 7 (StatSoft, USA).

Results and discussion

Mean air temperature during the 2009 vegetation period (May–September) was 15.8 °C, which is 2.1 °C above the long term average (1961–1990). Total rainfall was 277 mm, which is 31% below the long term average for the vegetation period at this site. The occurrence of extremely dry periods in the year 2009 was documented with the values of volumetric soil moisture (Fig. 1a). In the summer, the values of VPD were high due to high air temperatures (Fig. 1b), which increased evaporative demands of atmosphere on transpiration. The first irrigation was applied on July 16 (Fig. 1c). Needle water potential (Ψ) is a sensitive characteristic of water. We found significant difference of Ψ between the variants (Table 1). In case of IR variant, average value of Ψ did not fall below –0.6 MPa during the entire period, while in case of NIR variant average Ψ was

Table 1. Mean needle water potential (MPa) of NIR and IR group of spruce trees. Asterisks indicate significant differences ($P \leq 0.05$) between groups (ANOVA, Duncan's test).

	17.6.	29.7.	6.8.	27.8.
non-irrigated	–0.29	–0.98*	–1.39*	–1.31*
irrigated	–0.20	–0.25	–0.33	–0.56

reduced to –1.4 MPa, which indicates moderate drought stress.

During the evaluated period from July 16 to August 31 2009 (47 days), we observed significant differences between the transpiration of IR and NIR spruce trees in 21 days. On these days, the transpiration of NIR reached only 23% of the transpiration of IR trees. Significant differences in the transpiration of the two groups were found when SWC of NIR variant ranged from 10.38 to 13.7%. Mean SWC of IR trees was 21.9% over the entire assessed period. If VPD was equal or lower than 0.67 kPa, no difference was observed even if SWC decreased below 13.7%.

Significant differences between IR and NIR variants were observed between July 28 and July 31 (Fig. 1c). On these days the values of average VPD fluctuated between 0.89 and 1.19 kPa, which indicates enormous evaporative demands of the atmosphere. Significant differences in the transpiration of the two variants were also observed in the period from August 15 to August 22, which was characterised by extremely low SWC (below 10%). On August 21, we observed

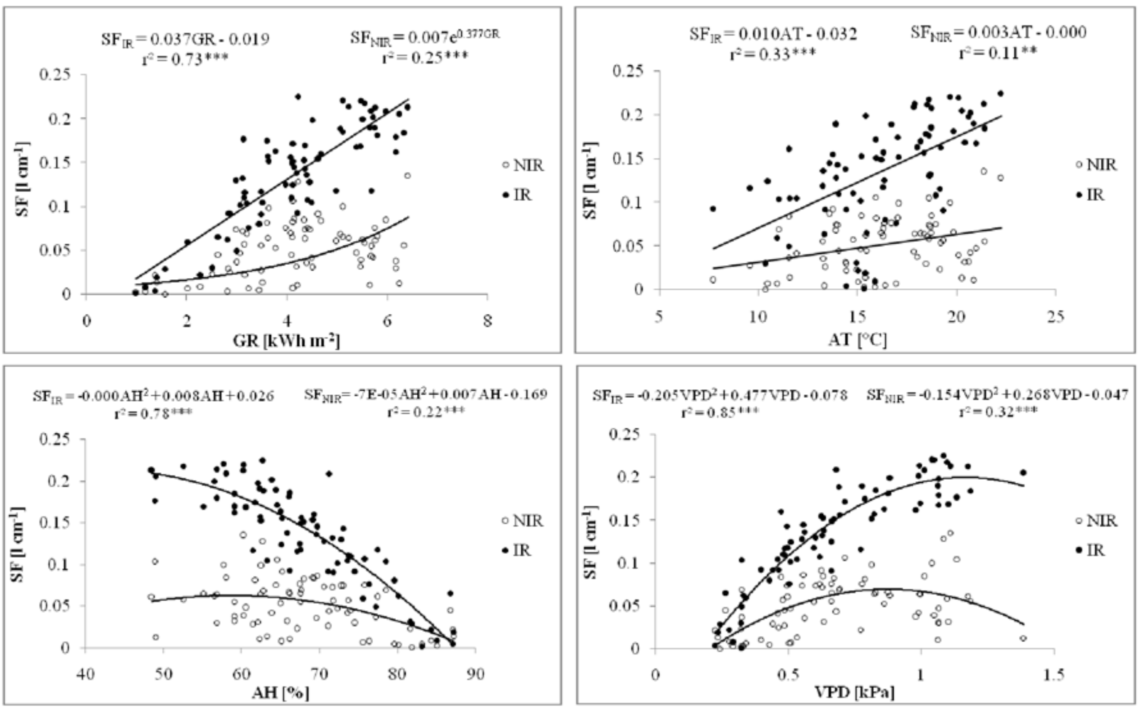

Fig. 2. Relationships between daily transpiration (SF) and daily values of global radiation (GR), air temperature (AT), relative air humidity (AH) and vapour pressure deficit (VPD) for different treatments (NIR and IR). $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

Table 2. Overview of the values of transpiration (SF) per 1 centimetre of stem circumference and for a mean tree of NIR and IR variants, cumulative transpiration deficit (KTD) and KTD_{red} reduced with stocking of 0.8 for the period from July 16 to August 31, 2009.

ΣSF_{IR} [L cm^{-1}]	ΣSF_{IR} [L tree^{-1}]	ΣSF_{NIR} [L cm^{-1}]	$\sum SF_{NIR}$ [L tree^{-1}]	SF_{NIR}/SF_{IR} [%]	KTD [L cm^{-1}]	KTD [mm]	KTD_{red} [mm]
8.46	467.0	3.41	188.2	40.3%	5.10	63.6	50.9

maximum difference between the average transpiration of the variants, while VPD was 1.38 kPa and SWC was 7.3%. This occurred after 8-day long rainless period. The differences between the transpiration of the variants were statistically significant, and the transpiration of IR trees was high, from the interval 0.22–0.26 L cm^{-1}.

Figure 2 presents the relationships between daily SF and meteorological parameters under the different regimes of water availability during the assessed period. Daily transpiration significantly responded to meteorological parameters in both variants (NIR and IR), although r^2 of NIR variant was markedly lower than that of IR variant for all meteorological parameters. The results prove that if soil is sufficiently moist, transpiration is primarily affected by evaporative demands of the atmosphere represented by VPD values. The dependency of transpiration to VPD was reduced as drought advanced (Fig. 2). The reason for the decreasing correlation to meteorological parameters with advancing drought is that if soil is drying and tissues are becoming dehydrated, stomata are closing, which reduces transpiration. Hence, soil water content becomes the principal factor of transpiration intensity. As Matejka et al. (2009) and Tesař at al. (2006) point out, high VPD accelerates transpiration particularly in the periods, when a forest is well supplied with soil water.

From the measurements of SF in sample trees of the two variants (NIR and IR) we estimated the transpiration of the experimental even-aged spruce stand in the pole stage. In Table 2 we present the amount of transpired water and KTD of IR and NIR trees or stands over the assessed period. On the last day of the experiment, KTD was equal to 5.10 L cm^{-1}. After the recalculation of the final KTD using stem circumference of the mean sample tree we found the difference between the transpiration of the mean NIR tree and IR tree equal to 278.8 L in 47 days (5.9 L day^{-1}). By converting this loss to per hectare values of a pole spruce stand we obtained a value of 63.6 mm ha^{-1}. After the reduction with stocking (0.8), KDT was reduced to 50.9 mm ha^{-1}. The total amount of the transpired water of the mean IR and NIR tree over the whole period was 467.0 L and 188.2 L, respectively (Table 2).

Lu et al. (1995) present that spruce transpiration at a non-irrigated plot was reduced at less than 25% of the transpiration of spruce trees at an irrigated plot. At our site Hriňová, mean transpiration of NIR group was 40.3% from the value of IR group in 47 days (Table 2).

Spruce tree species is very often negatively influenced by drought (Mauer et al. 2008). Overheating of tree capillaries on the stem by sun radiation can also affect water transpiration, causes water stress and results in predisposition for bark beetle attacks (Jakuš et al. 2011). In June 2003, Gartner et al. (2009) observed average transpiration totals of birch and spruce trees in a 20-year-old forest stand equal to 0.87 L cm^{-1} and 0.23 L cm^{-1}, respectively. Due to the advancing drought in August 2003, these values were reduced to 0.39 L cm^{-1} and 0.11 L cm^{-1}. On the days when transpiration indicated drought stress (i.e. when the difference between SF of IR and NIR variant was significant), we observed the average daily total of transpiration 0.22 L cm^{-1} in case of IR, and 0.05 L cm^{-1} for NIR variant. Lagergren & Lindroth (2002) state that in the period of extreme drought some spruce trees did not transpire at all. We did not observe such cases in our experiment. The authors present that the reduction of transpiration occurred after 80% of available water was depleted. Based on the results of several authors, spruce is considered to be a species which suffers from drought more than e.g. pine or beech. While the maximum average transpiration of a 50-year-old spruce was less than 1.5 mm day^{-1}, a pine tree of the same age reached a value of 2.5 mm day^{-1} (Lagergren & Lindroth 2002). In spite of this, spruce was more affected by drought than pine. Cienciala et al. (1997) measured transpiration values of mixed pine-spruce forests aged 50 and 100 years, and observed maximum of 2.8 mm and 1.7 mm, respectively.

Conclusions

In our study we found the threshold, when the transpiration of drought stressed spruce trees in the pole growth stage (NIR) started to be significantly different from the potential transpiration of irrigated trees (IR). We defined it from the point of SWC, which reached the values between 10.4 and 13.7% at the daily VPD greater than 0.67 kPa. The meteorological parameters influenced non-irrigated trees less than irrigated trees. This proved our assumption that under drought stress SWC becomes a limiting factor. Transpiration intensity of drought stressed trees was greatly limited on the days with high VPD values. Using cumulative transpiration deficit we revealed that the transpiration loss of the experimental even-aged homogeneous fully stocked spruce stand in the pole growth stage was 63.6 mm during the drought period.

Acknowledgements

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