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Assessing seasonal drought stress response in Norway spruce (*Picea abies* (L.) Karst.) by monitoring stem circumference and sap flow

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ABSTRACT

Summer drought frequency is expected to increase with climate change in forested regions of Europe. To examine the physiological impacts of low soil moisture on Norway spruce [*Picea abies* (L.) Karst.], we conducted an irrigation experiment in a Norway spruce-dominated forest. We monitored sap flow (Q_s), stem circumference and soil water potential (Ψ_w), measured needle water potential (Ψ_1), and estimated potential evapotranspiration (PET) in control and irrigated plots. Soil water availability influenced the response of Q_s to PET and the impact of Q_s on maximum daily stem shrinkage (MDS). The positive relationship between Q_s and PET was constrained below a threshold Ψ_w near -0.3 MPa. MDS was higher beyond this threshold, for a given value of Q_s . Higher MDS and lower tree water status (ΔW) were observed at low Ψ_w in control plants, suggesting the lower water potential of stems' conducting tissues. Stem circumference increase (SCI) was 62% lower in control trees following the irrigation treatment. Slight SCI recovery was observed in these trees in response to early autumn rainfall, which caused ΔW to return to its predrought state. The results demonstrate that low water availability not only reduced Q_s , ΔW , SCI, Ψ_1 and increased MDS but also altered their mutual relations. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS dendrometer; drought stress; Norway spruce; sap flow; tree water status

Received 10 October 2013; Revised 5 June 2014; Accepted 30 June 2014

INTRODUCTION

Soil water availability is an essential factor controlling the growth, physiology and distribution of Norway spruce (*Picea abies* (L.) Karst.) trees. In the context of ongoing climate change, periods of intensive drought are increasing in frequency (Allen *et al.*, 2010), causing stress that can lower the tolerance of Norway spruce to other adverse environmental factors. Lower elevations of the Western Carpathian mountain chain are affected by spruce forest decline (Jakuš, 2001). Among European conifers, Norway spruce exhibits relatively high sensitivity to water stress (Oberhuber and Mennel, 2010; Ge *et al.*, 2013). Consequently, spruce forest decline has been observed as a consequence of increasing drought severity (Mäkinen *et al.*, 2001). To develop a better understanding of Norway spruce sensitivity to drought stress, it is important to examine the hydraulic and physiological mechanisms governing drought response.

Transpiration, driven by the energy from solar radiation, is both a necessary consequence and a precondition for photosynthesis, the most fundamental process carried out by plants. Water demands for transpiration are supplied by sap flow. During periods of water shortage, assimilatory organs limit stomatal conductance and the synthesis of metabolites in photosynthetic processes (Lawlor and Cornic, 2002). This is subsequently reflected in physiological and growth processes, including the seasonally variable allocation of carbon to the stem. In many woody species, including Norway spruce, stem diameter measurements serve as useful indicators of drought and drought-induced reductions in growth rates (Zweifel *et al.*, 2006). Automatic dendrometers can also serve to elucidate the relationships between diurnal stem diameter variations and physiological processes in trees (Offenthaler *et al.*, 2001). Variations in stem circumference result from two main effects: (i) seasonal patterns of radial growth increment and (ii) dynamics of plant tissue water balance.

Seasonal stem growth is produced by actively dividing cells of the cambium. Xylem and phloem components are

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produced in the cambial zone by way of cell division, extension of primary cell walls, secondary wall formation and lignification. These processes are influenced by environmental factors (Deslauriers and Morin, 2005; Rossi *et al.*, 2006). Specifically, drought stress lowers leaf and conducting tissue water potential, cell turgor in the cambium zone, auxin and carbohydrate synthesis and transport of these substances into the cambium (Pichler and Oberhuber, 2007). Cell turgor itself promotes cellular enlargement, because it drives irreversible cell expansion and deposition of wall polymers (Proseus and Boyer, 2005). Stem size fluctuations also occur as water balance varies, because plants can temporarily use the water stored in their tissues (Herzog *et al.*, 1995; Čermák *et al.*, 2007). Tree tissues, including those of the stem, represent water reservoirs that can mitigate the effects of increased transpiration demands along and adjacent to the vascular pathway from the soil to the roots, stem, branches, assimilatory organs and the atmosphere.

To assess the drought response of Norway spruce, we set up an irrigation experiment in a young forest stand in Hriňová, Slovakia, with continuous monitoring of weather conditions, soil water potential, sap flow and stem circumference. Our main objective was to test the hypothesis that drought-affected Norway spruce trees would display lower tree water status (total stem shrinkage, ΔW), stem circumference increase (SCI) and Q_s (sap flow), but higher maximum diurnal stem shrinkage (MDS) than irrigated trees for a given potential evapotranspiration (PET). We further anticipated that the fundamental relationships among these variables would differ between trees of the control and irrigated treatments.

METHODS

Study site and tree species

This study was carried out in a 25-year old, pole-stage Norway spruce (*P. abies* Karst. L.) stand, at the Hriňová experimental site of central Slovakia (Stand 283-2; 48°35'N, 19°31'E, 655 m a.s.l.). The stand is closed, even-aged and homogeneous, with a 0.8-stocking level. Norway spruce accounts for 99% of the stand population, with the remainder composed of admixed European beech (*Fagus sylvatica* L.). The site is situated on a south-east facing slope with a 5% inclination. The soil is a Dystric Cambisol with a mean depth of 80 cm and a low stone fraction to a depth of 65 cm.

Two groups of trees were selected for an irrigation experiment. The first group of six trees was selected for a watering treatment, and the second group of six trees was selected as a control (i.e. no watering). One tree from the watered group was excluded from the data record, as this

tree exhibited poor health during the study year, with almost no growth and very low sap flow. Nearly undetectable growth and extremely low sap flow were also observed in this tree during 2010, which was an extremely wet year. Within the irrigated and control plots, individuals were located on microsites of ~5-m radius, with the centres of these circles spaced apart by about 15 m. The average DBH of the irrigated individuals was 18.6 cm, ranging from 15.4 to 21.7 cm. Average DBH of the control trees was 17.6 cm, with a range from 14.7 to 20.5 cm. Average tree heights were 17.2 m (16.3–18.2 m) and 16.9 m (14.8–18.2 m) in the irrigated and control trees, respectively.

The irrigation treatment began on 16 July and ended after the final watering on 27 August. A total of 23 m³ of water was used on 19 irrigation days. The water was transported from the water tank to the trees via tubes. Two rings of dripping tubes were placed around every individual, with perimeters of 1.0 and 1.5 m.

Meteorological data and potential evapotranspiration

Meteorological conditions were continuously monitored at an open plot, located 600 m north of the study site, at an elevation of 750 m a.s.l. Conditions measured included air temperature (°C), relative humidity (%), global incoming solar radiation [W m^{-2} ; Minikin TH (EMS Brno, CZ)] and rainfall [mm; MetOne 370 (Oregon, USA)]. Soil water potential (Ψ_w) was measured continuously, using gypsum blocks [MicroLog SP3 (EMS Brno, CZ)], capable of measuring tensions up to -1.1 MPa. Three blocks were installed at depths of 15 and 50 cm in both the irrigation and control plots, for a total of six blocks per group.

The Penman equation (Penman, 1948; Shuttleworth, 1993) was used to calculate PET (mm day^{-1}), as a measure of theoretical atmospheric evaporative demands unaffected by soil water deficiency:

$$PET = \frac{\Delta}{\Delta + \gamma} R_n + \frac{\gamma}{\Delta + \gamma} \frac{6.43 (1 + 0.536 U_2) D}{\lambda} \quad (1)$$

In Equation (1), Δ is the slope of the saturation vapour pressure curve, R_n is the net radiation [W m^{-2}], estimated as 85% of global incoming solar radiation [Monteith and Unsworth (2008) indicate albedo of coniferous forests around 0.16 and according to Shuttleworth (1993) albedo of unspecified tall forests is in the range of 0.11–0.16], D is the vapour pressure deficit ($e_s - e_a$) during the period (kPa), where e_a is the vapour pressure of free flowing air and e_s is the saturated vapour pressure at a given air temperature. The psychrometric constant, γ , was set at 62.4 Pa K^{-1} . The latent heat of vaporization (λ) was set at 2.45 MJ kg^{-1} (Allen *et al.*, 1998). We used a constant velocity of 1.5 m s^{-1} for the 2-m wind speed (U_2 , based on the data from the surrounding sites of Slovak Hydro-Meteorological Institute).

Leaf water potential and sap flow measurement

Leaf water potential (Ψ_l ; MPa) was measured on morning hours on current-year needles, by the psychrometric method, using a Psy Pro psychrometer (Wescor, USA). Sap flow was monitored in each tree by applying the stem tissue heat balance method (THB), as described by Čermák *et al.* (2004). The measured values are referenced to the initial stem circumference and reported in kilogrammes per centimetre of circumference per day ($\text{kg cm}^{-1} \text{day}^{-1}$). The data were recorded every 20 min, at a height of 1.3 m above the ground, using an EMS 51 sap flow sensor (EMS Brno, CZ). The THB method quantifies the amount of heat transported by water flow across a predefined area within the xylem conduit, as a percentage of the total heat supplied.

Stem circumference

Changes in stem circumference were monitored using automatic band dendrometers (DRL 26, ICT International, EMS Brno, CR), which were noninvasively fixed to the trees at a height of 2.5 m. A hard brush was used to remove dead material from the bark surface before installation. The measured values were referenced to the initial stem circumference and reported in micrometres per centimetre of circumference ($\mu\text{m cm}^{-1}$). Hourly mean values were derived from measurements taken at a 20-min interval.

The accuracy of dendrometers was tested by measuring the expansion and contraction of a sodium–potassium glass bottle with a circumference of 43 cm and a known contraction–expansion factor of $0.086 \mu\text{m cm}^{-1} \text{°C}^{-1}$. Within the 12 to 30 °C temperature range, expansion and contraction was linearly related to temperature change ($0.022 \mu\text{m cm}^{-1} \text{°C}^{-1}$). The highest daily temperature amplitude measured under the dense canopy of the Hriňová site was 12.8 °C. Given that the dendrometers and their bands were closely connected to stems, where the temperature amplitude would be even smaller, we did not adjust the dendrometer signal to account for the negligible impact of temperature variation.

We defined three phases of diurnal stem circumference changes, as described by Deslauriers *et al.* (2007): (1) the contraction (shrinking) period, from the morning maximum to the afternoon minimum; (2) the expansion (swelling) period, from the afternoon minimum to the morning maximum of the next day; and (3) the SCI, defined as the degree to which the stem circumference exceeded the previous morning maximum on the cumulative curve of circumference changes. Measurements began on 27 May. MDS was calculated as the difference between the morning (1–12 h) 1-h maximum (C_{max}) and afternoon (12–24 h) 1-h minimum. Tree water status (ΔW) was calculated separately for each tree, as the difference between the curve of SCI and the curve of maximum morning circumference (C_{max}) (Figure 1).

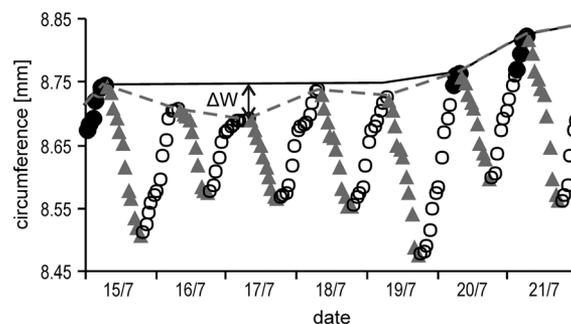


Figure 1. Average hourly stem circumference of Norway spruce tree and characteristic phases of the diurnal cycle during mostly sunny days. Grey triangles are used for the contraction (shrinking) period, with open circles used for the expansion (swelling). Solid black circles indicate the portion of the expansion phase during which the stem circumference exceeds the previous morning maximum (SCI). The dashed grey lines represent the maximum morning circumference curve, whereas the black growth curve represents SCI. Tree water status (ΔW) is shown as the difference between the SCI and maximum morning circumference curve.

RESULTS

Environmental conditions

Mean air temperature during the measured period (28 May–15 October) was 15.5 °C, which is 2.0 °C above the long term average (1961–1990). Total rainfall was 375 mm, which is almost equal to the long term average at this site. The rainfall events were irregularly distributed in time (Figure 2a). In response to dry conditions in May, soil water potential (Ψ_w) was near -0.6 MPa when the monitoring programme began on 28 May. Soil water potential was similar in the two plots before the onset of the irrigation treatment on 16 July. Thereafter, large differences in Ψ_w were observed between treatments, except following substantial rainfall events in early September. Soil water potential reached a minimum of -1.02 MPa (on 31 July) in the control plot during the irrigation period. The lowest Ψ_w values were observed after the end of the irrigation period, with a value of -1.1 MPa reached by 24 September in the control plot but not until 5 October in the irrigation plot. Thereafter, Ψ_w remained similar in the two plots.

Seasonal patterns of sap flow and daily stem shrinkage

Sap flow (Q_s) patterns were synchronous in the two plots before the irrigation treatment (Figure 2c). During the irrigation treatment, Q_s followed trends in PET (Figure 2b) in trees of the irrigation plot, but declined in the control plot. This was especially evident in July and August, when mean Q_s rates were up to four times higher in the irrigation plot than in the control plot.

Maximum daily stem shrinkage (MDS; Figure 2d) values were similar in the two plots before the irrigation treatment, except for slightly higher MDS in the control plot during a period of high PET and low Ψ_w in June. During the irrigation treatment, MDS was greater in trees

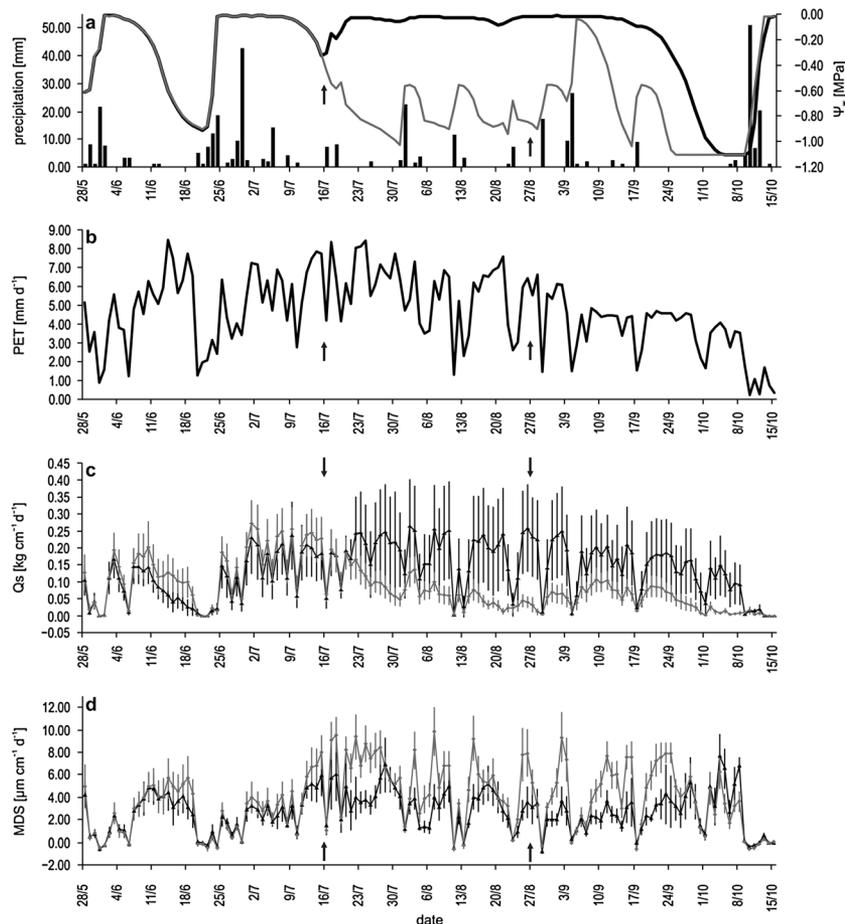


Figure 2. (a) Average daily values of soil water potential (Ψ_w) for irrigated (black line) and control (grey line) trees, daily rainfall totals (black bars), (b) course of daily potential evapotranspiration (PET), (c) course of daily average sap flow (Q_s) values (black – irrigated, grey – control, vertical lines representing 95% confidence intervals) and (d) Course of average values of maximum daily stem shrinkage (MDS) (black – irrigated, grey – control). Black arrows denote the beginning and end of the irrigation treatment.

of the control plot, especially on days with high PET. Following the completion of the irrigation treatment, MDS differences were conserved until early October. Thereafter, similar MDS was observed in the control and irrigated trees, except for higher values in the previously irrigated trees, as they reached their seasonal maximum values from 4 to 9 October.

Drought impacts on relations between PET, sap flow and daily stem shrinkage

The influence of soil water potential on the relationship between PET and Q_s was similar in both the irrigation treatment (Figure 3a) and the control plot (Figure 3b). The rise in Q_s with increasing PET was similar for all Ψ_w above -0.3 MPa. Below -0.3 MPa, increasing PET caused a smaller rise in Q_s . The influence of Ψ_w categories on Q_s variability was significant ($P < 0.05$), but interaction between Ψ_w and PET was the most important factor [$P < 0.0001$; analysis of covariance separate slopes model, with PET specified as the continuous predictor with

different slopes (effects) at different categories of Ψ_w]. This model explained 73% and 71% of the total variability in Q_s , in the irrigation and control plots, respectively. The smaller rise of Q_s with PET at lower Ψ_w categories is likely indicative of stomatal regulation of water loss, to mitigate the observed decline in needle water potential (Ψ_1 ; Figure 4). In the control plot, Ψ_1 declined from -0.18 MPa, at the beginning of the study period, to minima of -1.39 and -1.31 MPa on 6 and 27 August, respectively. In the irrigation plot, the lowest Ψ_1 observed during the irrigation period was -0.56 MPa, on 27 August. In the control plot, Ψ_1 was strongly positively related to Ψ_w , mainly to previous 14 days average ($R^2 = 0.93$, $P = 0.0076$, slope = 2.2832). In the case of irrigated plot, this relation had opposite slope was weaker and not significant ($R^2 = 0.51$, $P = 0.1745$, slope = -0.6331).

The relationship between PET and Q_s was similar between trees of the control and irrigation plots before the irrigation treatment (Figure 3c). During the irrigation phase, the increase in Q_s was smaller in the control plot

SPRUCE RESPONSE TO DROUGHT AND IRRIGATION EXPERIMENT

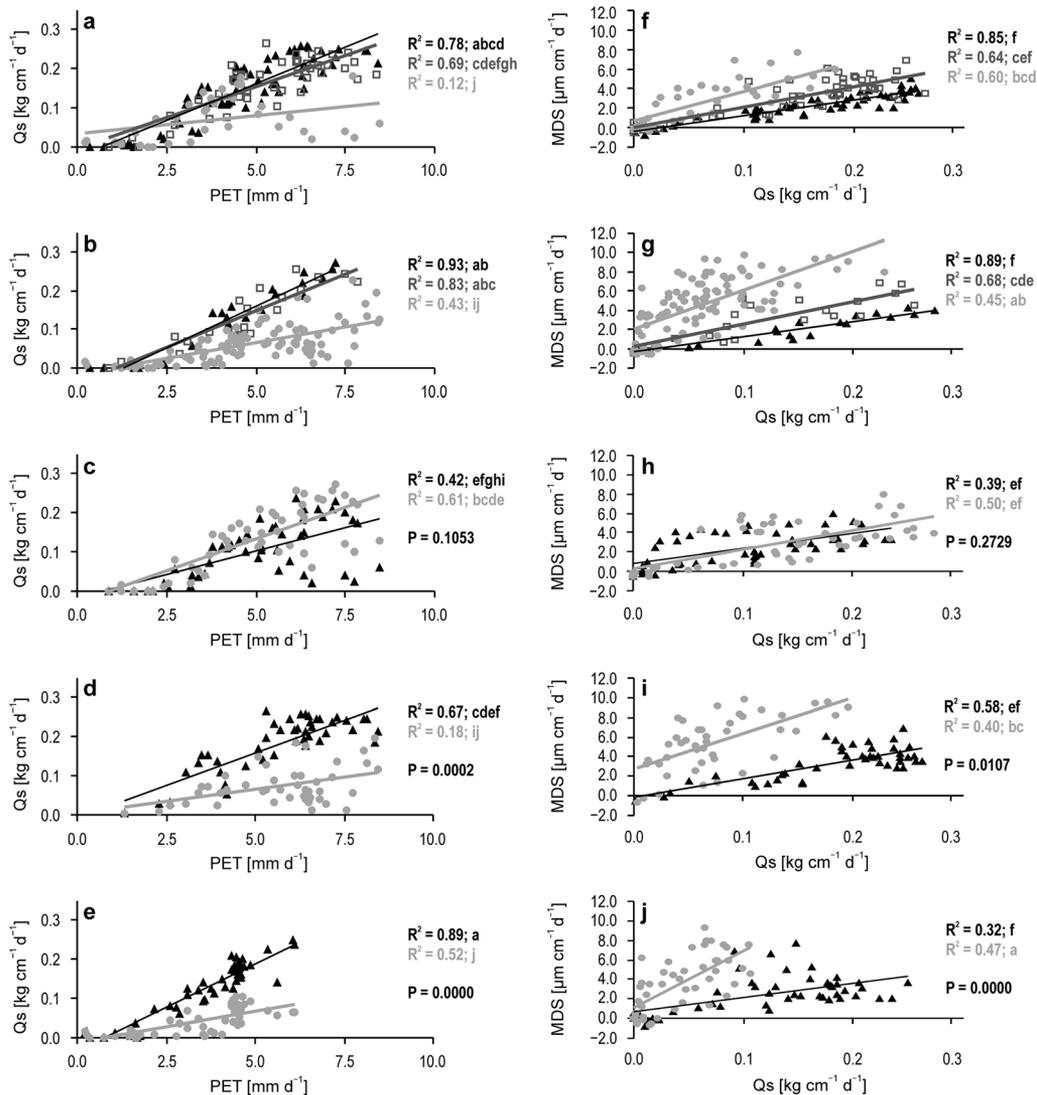


Figure 3. (a, b) Relationships between PET and average sap flow (Q_s) of irrigated (a) and control (b) trees for the following soil water potential (Ψ_w) categories: greater than -0.03 MPa (black triangles, fine black line); -0.03 to -0.3 MPa (open dark-grey squares, bold dark-grey line) and -0.3 MPa (light-grey circles, bold light-grey line). (c, d, e) Relationships between PET and average Q_s of irrigated (black triangles, fine black line) and control (grey circles, bold light-grey line) trees over periods before irrigation (c), during irrigation (d) and after irrigation (e). (f, g) Relationships between Q_s and average maximum daily stem shrinkage (MDS) in irrigated (f) and control (g) trees at the same soil water potential (Ψ_w) categories described above and over periods before irrigation (h), during irrigation (i) and after irrigation (j). R^2 is the coefficient of determination. The letters a, b and so on represent homogeneous groups of regression coefficients at $P < 0.05$ sorted from the highest regression coefficient, in alphabetical order. P = significance level of differences between regression coefficients before, during and after irrigation.

(test for homogeneity of regressions, $P < 0.01$; Figure 3d). No recovery was observed when irrigation was terminated, with regression coefficients remaining significantly different between the control and irrigation plots (Figure 3e).

Higher MDS values were observed at a given Q_s at low Ψ_w (less than -0.3 MPa) than at either intermediate (-0.03 to -0.3 MPa) or high Ψ_w (greater than -0.03 MPa). This pattern was observed in both the irrigation and control plots (Figure 3f and 3g) but was more pronounced in the latter. Interaction between Ψ_w categories and Q_s was the most significant factor in both groups ($P < 0.0001$; analysis of

covariance separate slopes model, with Q_s as the continuous predictor with different slopes (effects) at different categories of Ψ_w). The model explained 56% and 70% of the total variability in daily stem shrinkage in the control and irrigation plots, respectively. Before irrigation, the relationship between Q_s and MDS did not differ between the control and irrigation groups (Figure 3h). Thereafter, much lower MDS was associated with a given Q_s in trees of the irrigation plot ($P < 0.011$; Figure 3i), and this pattern was maintained when irrigation was halted ($P < 0.001$; Figure 3j).

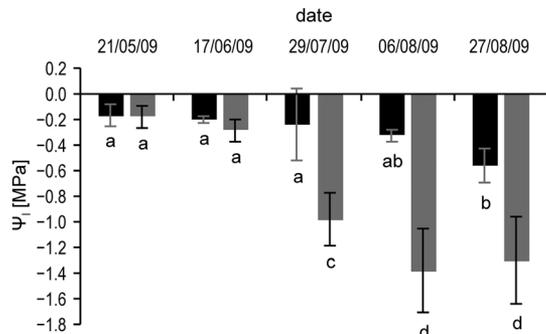


Figure 4. Average needle water potential (Ψ_n) of irrigated (black) and control (grey) trees and their 95% confidence intervals. The letters a, b and so on represent homogeneous groups, obtained by Duncan's test, at $P < 0.05$.

Seasonal patterns of stem circumference increase and tree water status

Stem circumference increase (SCI) was similar before the irrigation treatment, with just slightly higher SCI in the control trees (Figure 5a), consistent with sap flow observations. In trees of both treatments, little to no SCI occurred during a dry period in early June, but SCI increased in response to significant rainfall later in the month, so that 82% and 59% of total mean SCI (from 28 May) was completed in the control and irrigation plots, respectively, before the July onset of irrigation. SCI was generally higher in the irrigation plot during the irrigation treatment. SCI was negligible in August in the control group but rebounded slightly following wet periods in September and October.

Average SCI was 62% lower in the control than in the irrigation group from the onset of irrigation (16 July) to the end of the study period. Variability between treatments was 58.5% [$P = 0.006$, analysis of variance (ANOVA)] of total variability. The higher SCI after the irrigation treatment resulted in 15% higher SCI for the entire monitoring period

(28 May–15 October; (variability between treatments = 8.6%, $P = 0.381$, ANOVA).

Tree water status (ΔW) was very similar in the irrigation and control plots before the start of the irrigation treatment (Figure 5b). Although ΔW remained near $0 \mu\text{m cm}^{-1}$ in the irrigation plot throughout the irrigation treatment, trees of the control plot exhibited large decreases in ΔW during rain-free episodes. After irrigation had ceased, the ΔW of control group decreased more rapidly, and to lower values, during rain-free periods in September and October. Tree water status was correlated with Ψ_w in both the irrigated ($R^2 = 0.53$) and control groups ($R^2 = 0.60$).

DISCUSSION

Climate change is expected to result in more frequent and severe drought in many parts of Europe. Understanding the relationships between soil water dynamics and tree water use is hence essential for current as well as future forest management (Klein *et al.*, 2012). In a Norway spruce stand of central Slovakia, we found that low soil water potential resulted in lower needle water potential, reduced sap flow, lower tree water status, greater daily stem shrinkage and reduced stem circumference increase, with only partial recovery in response to late season rainfall. According to climatic scenarios, in comparable forest vegetation zones of Czech Republic and Slovakia, Hlásny *et al.* (2011) predict significant spruce production decrease of 25% for the period 2071–2100, as a result of expected increase of aridity (water deficit 50–150 mm) more favourable for deciduous tree species (beech, maple and ash; Škvarenina *et al.*, 2004).

The impacts of water availability on sap flow and stem circumference

The maximum potential rate of transpiration, which drives sap flow, is determined by ambient atmospheric conditions,

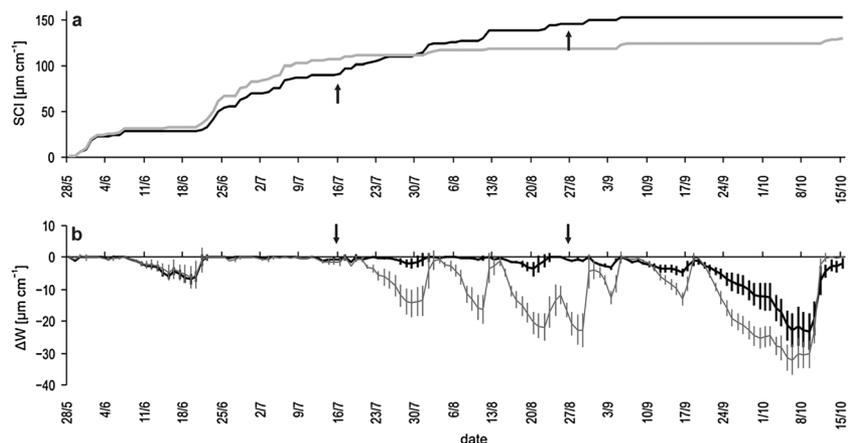


Figure 5. (a) Average stem circumference increase (SCI) for irrigated (bold black) and control (bold, grey) trees. Black arrows denote the beginning and end of the irrigation treatment. (b) Average tree water status (ΔW) in irrigated (black) and control (grey) trees. Vertical lines represent 95% confidence intervals.

including vapour pressure deficit, photosynthetic photon flux density, temperature and CO₂ concentration (Cruiziat *et al.*, 2002). At Hriňová, sap flow (Q_s) followed patterns of PET when soil water potential (Ψ_w) was high. However, when Ψ_w decreased to below -0.3 MPa, the increase of Q_s with PET was less pronounced (Figure 3a and 3b) likely because of stomatal control of water loss by transpiration.

Moreover, during the period before irrigation started, the group of afterward irrigated trees tended to have lower Q_s (Figures 2c and 3c), although except 1 day statistically not significant. This was reflected especially during Ψ_w decrease and high PET (Figure 2a and 2b) in the second decade of June, suggesting higher sensitivity of irrigated trees to these conditions. This could bring uncertainty to later comparison of both groups and most probably diminish differences between them (Figures 2c and 3d and 3e).

Maximum Q_s is related to the hydraulic resistance of the entire pathway from roots to leaves, as well as the capacity to lower needle water potential (Ψ_1 ; Deslauriers *et al.*, 2007). The lowest Ψ_1 observed at Hriňová was -1.39 MPa in the control group and -0.56 MPa in the irrigation group. Similarly, Cenciala *et al.* (1994) reported a minimum predawn Ψ_1 value -1.2 MPa in drought-stressed Norway spruce trees. Lu *et al.* (1996) observed that Ψ_1 remained above -2.0 MPa under more prolonged drought conditions. Relationships between Q_s and MDS were similar in the control and irrigation plots before the irrigation treatment (Figure 3h), but differences were apparent during and after the irrigation period (Figure 3i and 3j).

In accordance with the cohesion-tension theory, transpiration contributes to the gradient of water potential, which is the driving force (Nadezhkina *et al.*, 2010) controlling the rate of sap flow along tree stems from the roots toward the assimilatory organs (Wei *et al.*, 1999). Water molecules in wood conduits are arranged in thin columns, bound by cohesion forces and follow the direction of decreasing water potential toward assimilatory organ. As a result of adhesion forces, this tension is transferred to cell walls, reducing their diameter (e.g. Irvine and Grace, 1997; Perämäki *et al.*, 2005). Diameter reduction can also result from reduced turgor in the more elastic phloem and in the outermost nonlignified tree ring tissues (Herzog *et al.*, 1995; Abe *et al.*, 2003). The gradient of water potential between the conductive wood areas and the phloem results in lateral water exchange (Sevanto *et al.*, 2011). Meanwhile, as transpiration occurs, a peristaltic wave of diameter variation progresses downward, with a time delay, from the assimilatory organs to the stem (Sevanto *et al.*, 2002) and roots (Génard *et al.*, 2001), resulting in observable diurnal patterns of stem diameter variation.

Tree water status

Tree water status (ΔW) was correlated with Ψ_w at Hriňová. This observation is consistent with the previous research

that has demonstrated a close relationship between atmospheric evaporative demands, Ψ_w and ΔW in Norway spruce (Zweifel *et al.*, 2005, 2007). Decreasing ΔW is known to reflect decreasing water potential within the storage tissues of the stem, which can result in a stem shrinkage over several weeks, even during the wood growth period (Zweifel *et al.*, 2006). Stem shrinkage is reversed only after water absorbed by roots or stored in tissues with higher water potential eliminates the water deficit in the stem or xylem (Offenthaler *et al.*, 2001). Both Ψ_w and ΔW increased in the control plot following rain events (e.g. 13 August and 17 September; Figures 2a and 5b). High MDS values were subsequently observed in the control plot (14–16 August and 18–24 September; Figure 2d), as ΔW returned to lower values (Figure 5b). Thereafter, MDS values were very similar to the irrigated group but at lower ΔW . This means permanent stem shrinkage in the control trees.

Water stored in xylem and phloem tissues can meet the transpirational requirements of certain trees for as much as a week (Čermák *et al.*, 2007). Spruce seedlings have been shown to use 10–65% of these water reserves daily, depending on transpirational demands (Zweifel *et al.*, 2001). We postulate that, in response to low water availability, control trees at Hriňová not only reduced Q_s but also increased the rate of stored water to support daily transpirational needs. This resulted in lower Ψ_{stem} and ΔW , because of higher MDS and limited swelling.

Seasonal patterns of stem circumference increase

Stem circumference change reflects the net effect of cell turgidity change in the cambial zone, coupled with the development and growth of xylem and phloem (Abe and Nakai, 1999; Abe *et al.*, 2003). Cell expansion is driven largely by turgor pressure, which irreversibly deforms the cell wall as the cell compartment expands (Lockhart, 1965). At the seasonal timescale, stem circumference increase (SCI) is largely associated with growth processes, especially those associated with new tree ring formation. This process is highly sensitive to water deficit in Norway spruce (Cenciala *et al.*, 1994), because of the impact of drought stress on cell division and tracheid growth (Abe *et al.*, 2003). Periodic drought stress, especially in late summer, results in high temporal growth variability in spruce trees even of the subalpine zones of eastern Europe (Wilson and Elling, 2004) and also of south-western Germany (Spiecker, 1990). The main growth period has shifted from June–August (pre-1900) to May–July in these altitudes, as a consequence of a warmer climate (Büntgen *et al.*, 2006).

In a Slovenian Norway spruce stand, Gričar and Čufar (2008) found that cambial activity ceased before August during the European drought of 2003, whereas phloem

formation ceased in mid August and wood formation ended at the beginning of September. Enhanced late season growth has been observed in temperate conifers when moist conditions follow severe drought before dormancy (Letts *et al.*, 2009). At Hriňová, more than half of SCI occurred before the onset of the irrigation treatment. Thereafter, SCI increased much more quickly and to a greater extent in trees of the irrigation plot. SCI did not increase after 4 September in trees of the irrigated plot. In control trees, drier conditions resulted in very little SCI during August, but partial recovery was observed in September and October, in response to rainfall events. Late season SCI may have been associated with increased turgidity or late wood formation. Rossi *et al.* (2007) report that cell prolongation, wall formation and lignification processes can continue until mid-October.

CONCLUSIONS

The results of this irrigation experiment quantify the physiological impacts of moderate drought stress on Norway spruce. Sapflow closely followed variations in PET only when soils were moist. The response of Q_s to increasing PET was constrained below a threshold Ψ_w near -0.3 MPa, whereas MDS tended to increase following decreasing Ψ_w , for given values of Q_s . The higher MDS and lower ΔW values of control trees suggest (i) increased use of water storage in tree tissues, to facilitate daily transpirational needs, and (ii) lower needle water potential (Ψ_1), which is required for the maintenance of a favourable water potential gradient from the roots to the assimilatory organs. Reduced water availability caused much lower ΔW and SCI, the former recovered to its predrought state in control trees following rainfall events in September and October, and this was reflected in a small degree of SCI compensation.

ACKNOWLEDGEMENTS

This work was supported by the Slovak Research and Development Agency (Contracts APVV-0022-07, APVV-0436-10, APVV-0482-12) and the Grant Agency of the Ministry of Education and the Slovak Academy of Sciences (VEGA 0160-09, VEGA 0034-14).

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