

Concomitant dendrometer and leaf patch pressure probe measurements reveal the effect of microclimate and soil moisture on diurnal stem water and leaf turgor variations in young oak trees

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Abstract. Tree water relations and their dependence on microclimate and soil moisture were studied over several months in young oaks (*Quercus robur* L.) subjected in large lysimeter-based open top chambers to environments with a controlled soil water supply. Automated single point dendrometers and the recently developed leaf patch clamp pressure (LPCP) probe were used for monitoring water-related stem radius variations (ΔW) and turgor-dependent leaf patch pressures (P_p). Both parameters showed distinct diurnal patterns with sharp negative and positive peaking of ΔW and P_p , respectively, after solar noon and recovery to initial levels in the evening. During the day, varying solar radiation was responsible for short time fluctuations of P_p in the range of minutes to hours reflecting feedback regulation of leaf turgor by sunlight driven stomatal movements. At longer timescales, i.e. days to months, atmospheric vapour pressure deficit (VPD) and soil water content (SWC) were the main determinants of ΔW and P_p . Daily minimum and maximum values of ΔW and P_p decreased and increased, respectively, with increasing VPD or decreasing SWC and recovery of ΔW and P_p in the evening was impeded by low SWC. In well-watered oaks, daily positive peaking of P_p preceded daily negative peaking of ΔW ; these time lags gradually increased with increasing soil drought, suggesting hydraulic uncoupling of stem and leaves.

Additional keywords: drought, solar radiation, stem radius variation, stem water storage, tree water relations, vapour pressure deficit.

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Introduction

Plant water relations are fundamental determinants in plant physiology, affecting a wide range of biochemical reactions and physiological functions. Water serves as the physicochemical environment for cellular processes, is required for maintaining cellular turgor and acts as universal solvent for long-distance transport of mineral nutrients, assimilates and secondary metabolites (cf. Kramer 1983). Water shortage causes severe stress, which limits photosynthetic carbon sequestration and through this, growth and biomass allocation (Boyer 1982; Kaiser 1987; Chaves *et al.* 2003). The way in which plants respond to this environmental constraint depends largely on their hydraulic architecture, which controls plant water relations, particularly the balance between soil water uptake and transpirational water loss.

In contrast with most herbaceous plants, the hydraulic architecture of tall trees is much more complex, comprising a broad array of interacting mechanisms controlling soil water uptake, long-distance transport, internal water storage and transpirational water loss (Meinzer *et al.* 2001). Trees, for example, are capable of counterbalancing temporal water deficits by withdrawing water from their voluminous stems and branches, which are considered as fast accessible storage pools when canopy water loss exceeds soil water uptake by roots (Tyree and Yang 1990; Čermák *et al.* 2007; Westhoff *et al.* 2009). Such internal water reallocation provides an adaptive advantage that allows trees to minimise stress during short periods of drought. Recent physiological tree models integrate stem water storage pools into an extended hydraulic

system, thus providing better predictions for tree water relations and their changes in response to environmental fluctuations (Steppe *et al.* 2006; Zweifel *et al.* 2007). Nevertheless, there is still some uncertainty in defining water relations in trees, probably because of the highly complex nature of this system and inherent technical limitations.

Plant water relations can be investigated by measuring environmental parameters, e.g. atmospheric vapour pressure deficit (VPD) and soil moisture content, or more reliably by analysing physiological parameters which depend on plant water content (Remorini and Massai 2003; Zweifel *et al.* 2007). Leaf and stem water potential (McCutchan and Shackel 1992; Ferreira *et al.* 1997; Gebre *et al.* 1998) and xylem sap flow (Wullschlegel *et al.* 1998; Fernández *et al.* 2001; Čermák *et al.* 2007) are frequently used indicators reflecting tree water content at the whole-plant level. However, these techniques are inadequate in providing easily accessible information on stem water storage and its linkage with the water demand of transpiring leaves that is crucial for a more thorough understanding of tree water relations and their responses to environmental fluctuations. Earlier attempts to derive information on stem water storage from sap-flow data and to link it with leaf transpiration were based on extensive technical instrumentation or theoretical considerations that are applicable only to single trees (Steppe *et al.* 2006; Čermák *et al.* 2007). Such limitations might be overcome by combining less sophisticated, leaf and stem specific approaches, thus, allowing concomitant measurements of stem and leaf water status in numerous trees.

Dendrometer measurements of diurnal stem radius variations can provide specific information on the relative stem water content as these dimensional changes are directly related to the diurnal dynamics of water storage depletion and replenishment in elastic stem tissues (Zweifel *et al.* 2000, 2001; Meinzer *et al.* 2001). Thus, dendrometer measurements mainly reflect changes in the water content of the elastic bark rather than in the water content of the inelastic wood. Diurnal stem radius variations have been shown to be very sensitive indicators of tree water deficits, revealing small changes in stem water content with high temporal resolution (Goldhamer and Fereres 2001; Remorini and Massai 2003). Concomitant analysis of leaf water status may allow for a better understanding of internal regulation of tree water balances explaining the functional relationship between stem water storage and transpirational water loss. Measurements of diurnal leaf patch pressure variations using the recently developed leaf patch clamp pressure (LPCP) probe technique can be used as indicator for leaf turgor, providing specific information on temporal leaf water deficits (Zimmermann *et al.* 2008, 2010; Rüger *et al.* 2010).

In the present study, we took advantage of automated single point dendrometers and online-operating LPCP probes to monitor the diurnal patterns of water related stem radius variation (ΔW) and turgor-dependent leaf patch pressure (P_p). We applied both techniques to young oak trees growing in large, lysimeter-based open top chambers (OTCs) with two different irrigation regimes. The aims of the study were to: (i) evaluate the dependency of diurnal stem and leaf water changes on short- and long-term fluctuations of microclimate

variables; (ii) test the effect of drought on diurnal stem and leaf water variations; and (iii) gain a deeper insight into the functional relationship between the diurnal dynamic of stem water storage and the water demand of transpiring leaves.

Materials and methods

Experimental design and plant material

The study was conducted in the model ecosystem facility of the Swiss Federal Research Institute WSL, Birmensdorf, Switzerland (47°21'48"N, 8°27'23"E, 545 m above sea level). The research facility was comprised of 16 open top chambers (OTCs) with a height of 3 m and a plantable soil surface area of 6 m². Below ground, each OTC had concrete-walled lysimeter compartments with a depth of 1.5 m. Each lysimeter contained a 50-cm drainage layer of pure quartz gravel, covered by an 85-cm layer of acidic Haplic Alisol subsoil and a 15 cm layer of topsoil (loamy sand, pH 4.1). Natural precipitation was excluded from the OTCs by retractable glass roofs closing automatically at the onset of rain fall. In spring 2006, 2-year-old oak saplings (*Quercus robur* L.) were transplanted into the OTCs and grown with sufficient water supply for one season to ensure successful establishment. Repeated drought treatments were applied during the following 3 years (2007–09), with four OTCs assigned to drought treatments and four OTCs assigned as controls. In the drought treatment, soil water supply was reduced during the growing season by temporary interruption of the irrigation. All measurements described in the present study were performed on one selected oak tree per OTC during the growing season 2009 with one dendrometer and two LPCP probes per tree. LPCP probe measurements were recorded in 'universal time co-ordinated' (UTC). To compare the different results all measurements were converted to 'central European summer time' (CEST).

Measurement of soil water content and microclimate

Volumetric soil water contents (SWC; m³ m⁻³) were measured by time domain reflection (TDR 100; Campbell Scientific Inc., North Logan, UT, USA) in each lysimeter compartment at 12, 38, 62 and 88 cm depth. Air temperature and air RH were measured with shaded EL-USB-2 data loggers (Lascar Electronics Ltd, Salisbury, UK) in each growth chamber at 120 cm height at intervals of 1 h. Solar radiation (SR; W m⁻²) outside the growth chambers was continuously monitored with a SP-LITE Silicon Pyranometer (Kipp and Zonen, Delft, The Netherlands).

Measurements of leaf water potential and cell turgor

Predawn leaf water potentials were determined by measuring balancing pressure values (P_b ; MPa), i.e. the pressure at which water appeared at the cut end of a leaf upon pressurisation, using a Scholander pressure chamber (M 600, Mosler Tech Support, Berlin, Germany). Cell turgor measurements (P_c ; kPa) were performed as described in detail elsewhere (Zimmermann *et al.* 1969; Zimmermann 1989). The microcapillary of the turgor probe was inserted from the abaxial side of the leaves into the symplast of parenchymal cells close to the main vein.

Monitoring of stem water changes

Variations in relative stem water content were derived from measurements of water-related swelling and shrinking of elastic stem tissue (ΔW ; μm) using automated single point dendrometers (Zweifel Consulting, Hombrechtikon, Switzerland). The dendrometers were mounted on aluminium frames fixed with three stainless steel rods to the stem base at 10 cm above ground. Readings of the dendrometers were taken at 1-min intervals, averaged every 10 min and recorded by a data logger (Campbell Scientific Inc.). The resolution of the dendrometer measurements was $\sim 10 \mu\text{m}$ (including temperature dependent variation). To distinguish water-related radius changes from growth-induced radius changes, dendrometer recordings were de-trended for growth according to Zweifel *et al.* (2005) with slight modifications (Fig. 1). Briefly, a ‘growth line’ was constructed by drawing a horizontal line from each daily stem radius maximum in the morning (P1; beginning of stem shrinking) to the next equal stem radius value in the evening (P2; stem radius recovery), spanning a daily cycle of water-related stem radius contraction and expansion. Between each contraction–expansion cycle the growth line followed the original dendrometer records representing the daily stem growth. In drought-treated trees, where daily stem radius recovery was incomplete due to permanent shrinkage of the stem, the growth line spanned longer time periods without following the original dendrometer records. The differences between the constructed ‘growth line’ and the original dendrometer records were considered as relative measures of daily stem water deficits or in the case of drought-treated trees as long-term stem water deficits. These differences were plotted as the instantaneous values of ΔW (μm).

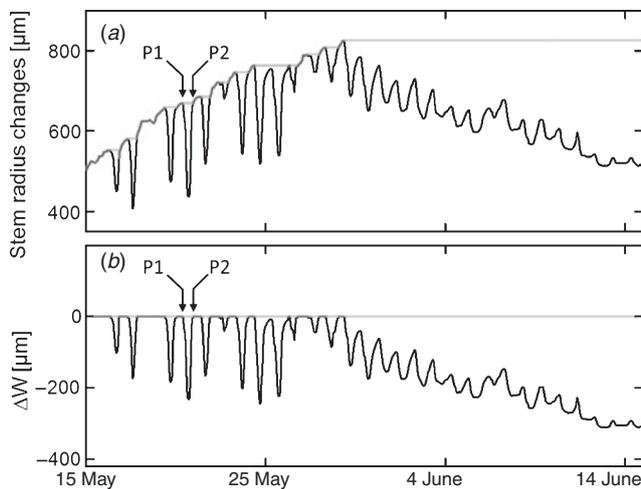


Fig. 1. De-trending the dendrometer records for growth. (a) Original measurements of stem radius changes (black line) with a fitted ‘growth line’ (grey line). (b) Stem water deficits (ΔW), as the difference between the ‘growth line’ and the original dendrometer records. The symbols P1 and P2 indicate the beginning of daily stem radius shrinking in the morning and the stem radius recovery in the evening, respectively. Incomplete stem radius recovery in the evening indicates a permanent stem water deficit.

Monitoring of relative leaf turgor pressure

The principle of the magnetic leaf patch clamp pressure (LPCP) probe is described in detail elsewhere (Zimmermann *et al.* 2008; Westhoff *et al.* 2009). Briefly, a relatively small covered patch of an intact leaf is used as a sensing element for measuring turgor pressure changes in the uncovered surrounding. Precondition is that the patch is in hydraulic (osmotic) contact with the entire leaf and that the stomata of the patch are closed in order to avoid water loss from the patch. This is achieved by clamping an intact leaf between upper and lower circular metal pads that are integrated in a magnet. The upper magnet is movable. Thus, the magnetic pressure, P_{clamp} , exerted on the leaf patch can be altered by changing the distance between the two magnets. This allows proper adjustment of P_{clamp} to leaf thickness and rigidity. P_{clamp} is kept constant during the measurements. The turgor pressure in the leaf patch is opposed to the magnetic pressure. This has the consequence that the output pressure P_p sensed by a pressure sensor integrated in the lower magnet is low at high turgor pressure and *vice versa* high at low turgor pressure (P_c):

$$P_p = \left(\frac{b}{aP_c + b} \right)^{\frac{1}{a}} \cdot F_a \cdot P_{\text{clamp}}, \quad (1)$$

where a and b are leaf-specific, elastic constants and F_a is a leaf-specific attenuation factor which takes into account that part of P_{clamp} is used for compression of air-filled spaces and structural elements such as cuticle and cell walls. Measurements on various plant species have shown (Zimmermann *et al.* 2008; Westhoff *et al.* 2009) that F_a can be assumed to be constant down to very low turgor pressures ($\sim 50 \text{ kPa}$), even over long measuring periods (Zimmermann *et al.* 2010). The probes and the components for telemetric and mobile network-based data transfer to the internet were purchased from ZIM Plant Technology GmbH (Hennigsdorf, Germany).

Results

Calibration of the LPCP probe using the cell turgor pressure probe

The theory underlying the LPCP probe predicts that the output patch pressure (P_p) is a power function of the turgor pressure (P_c). This could be verified by concomitant P_p and P_c measurements on neighbouring leaves of a single tree (Fig. 2). It is obvious that the data points could be fitted quite well with Eqn 1 using appropriate values for the elastic constants a and b . Additional measurements of balancing pressure (P_b) on leaves located close to the measuring sites of P_c and P_p yielded a linear dependency between P_p and P_b (inset Fig. 2), indicating that P_b values in *Q. robur* depend on P_c .

Diurnal stem and leaf water changes and their dependency on microclimate

Both, relative stem water content (ΔW) and P_p showed distinct diurnal patterns with a sharp decrease or increase, respectively, in the early morning and minimum or maximum peak values, respectively, in the afternoon (Fig. 3a, b). In the evening, both parameters recovered to their initial morning levels and remained

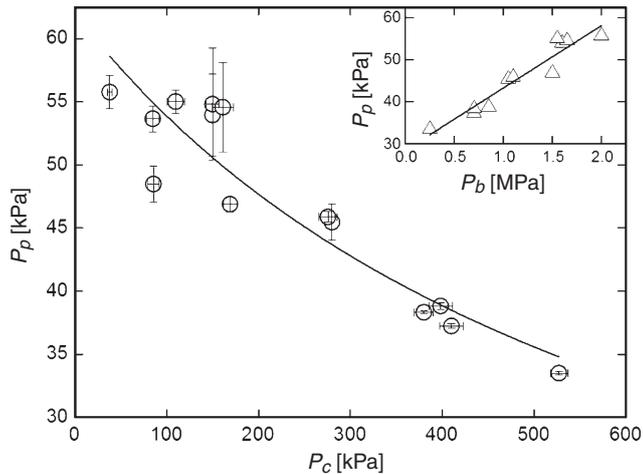


Fig. 2. Concomitant measurements of the leaf patch clamp output pressure (P_p) and the cell turgor pressure (P_c) on leaves of a well-watered tree. Each P_c data point represents the mean (\pm s.d.) of 5–15 P_c values taken from 2–5 min recordings; each P_p data point represents the mean (\pm s.d.) of the P_p values recorded during the P_c measurements. The dependency of P_p on P_c could be fitted by Eqn 1 using appropriate values for the constants ($F_a=0.3$, $P_{c\text{clamp}}=207$ kPa, $a=1.1$, $b=660$ kPa; $r^2=0.81$). Inset: Plot of the P_p values against the corresponding P_b values. Since the tree was small and in turn, the number of leaves was limited, only single spot measurements could be performed. Despite this, data could be fitted with a straight line (using the least square method; $r^2=0.91$).

nearly constant overnight. P_p frequently showed overshooting values (additional peaking) in the late morning hours, probably due to a lag in stomatal closure that caused further leaf turgor loss (Figs 3*b*, 4*a*). The observed diurnal patterns of ΔW and P_p were mostly concomitant with diurnal changes in microclimate, i.e. solar radiation (SR), air temperature and atmospheric VPD. The daily maximum values of P_p (corresponding to minimum turgor values) did not coincide with minimum values of ΔW , i.e. positive peaking of P_p generally preceded negative peaking of ΔW . The average peaking times (\pm s.d.) were 90 min (± 60 min; $n=8$) and 170 min (± 53 min; $n=4$) after solar noon for P_p and ΔW respectively. On cloudy days, temporary fluctuations of SR resulted in synchronous P_p changes (Fig. 3*a*) whereas no such responses were observed on sunny days (Fig. 3*b*). In contrast with P_p , ΔW did not show any short time responses to fluctuating SR.

Diurnal patterns of ΔW and P_p in well-watered oaks (soil water content >14%; 62 cm depth) strongly varied during the measurement period reflecting a clear dependency on the daily weather conditions. On days with high VPD, ΔW and P_p showed lower minimum and maximum peak values, respectively, than on days with low VPD (Figs 3*a*, *b*, 4*a–c*). However, compared with P_p , ΔW reacted with a higher sensitivity to VPD, as exemplified between 15 and 18 August by the steeper decline of ΔW in line with gradually increasing VPD (Fig. 4*a–c*). Further, diurnal changes of ΔW were not observed on days with exceptionally low VPD (≤ 10 hPa) while leaves maintained substantial diurnal P_p changes. Similar recordings were obtained on other well-watered trees (data not shown).

Responses of diurnal stem and leaf water changes to drought

Soil water shortage had a strong influence on the long-term trends of ΔW and P_p . Night plateau values of ΔW and P_p decreased and increased, respectively, with ongoing soil drought (soil water content <14%), indicating gradual water loss in leaves and stems (Fig. 5). Daily negative peaking of ΔW diminished with increasing drought whereas daily positive peaking of P_p was apparently not affected. Re-watering after prolonged soil drought periods resulted in a rapid recovery of the initial night values of ΔW and P_p and restored daily negative peaking of ΔW (Fig. 5). Closer inspection of datasets from different trees at a shorter time scale revealed different response times of both parameters to re-watering (Fig. 6; Table 1). The P_p values in leaves of trees subjected to drought showed first responses to re-watering within 1 h and night-values recovered completely within 1 day after the onset of irrigation. Irrigation on subsequent days had no further effect on P_p indicating that the leaf water status recovered completely after 1 day. In contrast, ΔW in stems of drought subjected trees showed first responses to re-watering after 2–5 h and full recovery was reached 1–3 days after the onset of irrigation. The kinetics of ΔW recovery correlated well with the kinetics of soil water content (SWC) recovery at 12 cm depth. SWC measured at this soil depth also increased stepwise and a plateau value was reached 3 days after first re-watering.

Prolonged drought increased the time lags between daily negative peaking of ΔW and positive peaking of P_p (Δt), mainly due to later peaking of ΔW . In well-watered trees (predawn P_b values <0.5 MPa), Δt ranged from –2 to 10 h and the modal value of the Δt distribution was 2 h (Fig. 7*a*). In drought-subjected trees, the width of the Δt distribution increased with decreasing P_b values (Fig. 7*b–d*). For trees subjected to moderate drought stress (predawn P_b values 0.5–1.5 MPa) the modal value was still around 2 h, but larger Δt values (of up to 12 h) were more frequently observed. At severe drought stress (predawn P_b values >1.5 MPa) the width of the Δt distribution was extremely broad, with Δt values ranging from 1 to 15 h and the modal value of the Δt distribution shifted to 7 h.

Discussion

Information on the hydraulic relationship between stem and leaves is crucial for a thorough understanding of tree water relations and their responses to environmental fluctuations. In the present study we took advantage of automated single point dendrometers and the recently developed LPCP probe to monitor diurnal patterns of water-related stem radius variations (ΔW) and turgor-dependent leaf patch pressure (P_p) in young oak trees grown with a controlled soil water supply. Measurements were performed in parallel over several months reflecting the impact of microclimatic variables and soil moisture on tree water relations. The reliability of the recently developed LPCP probe for measurements on oak leaves could be verified by concomitant cell turgor measurements using the well acknowledged cell turgor pressure probe technique (Zimmermann *et al.* 2004). Parallel pressure bomb experiments performed revealed a very good correlation between the LPCP probe measurements and

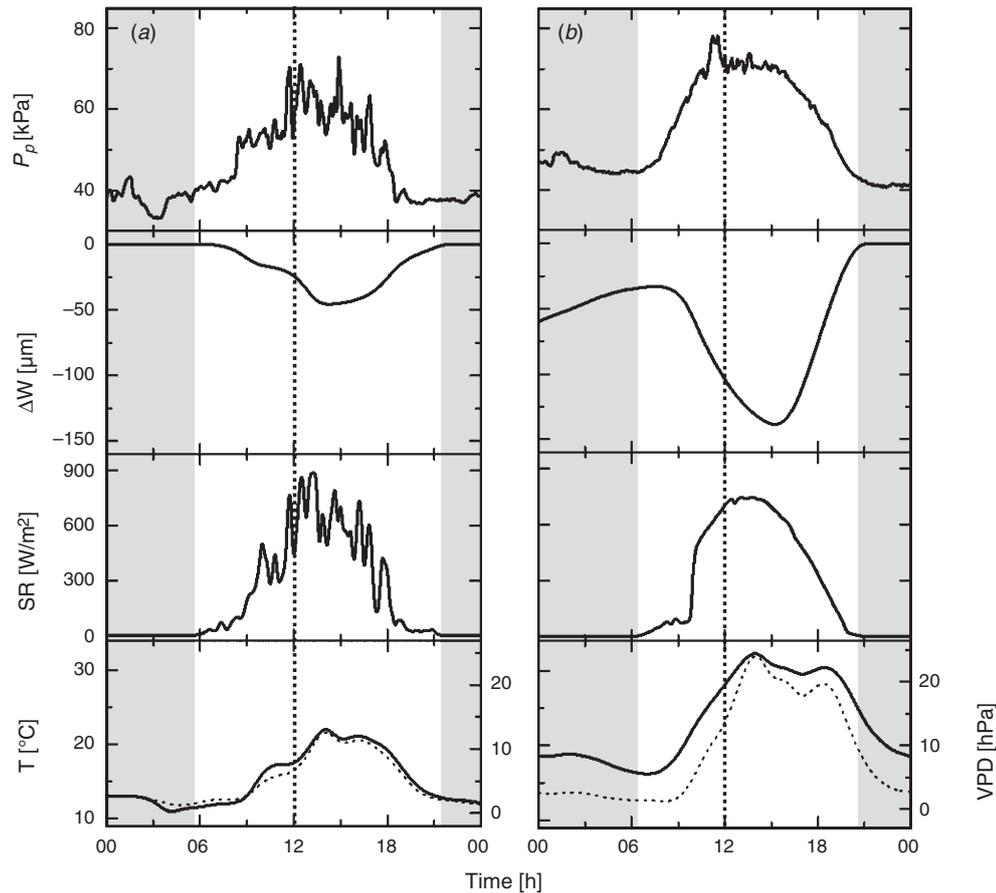


Fig. 3. Concomitant measurements of diurnal patterns of P_p and ΔW on a well-watered tree together with solar radiation (SR), air temperature (T; solid line) and vapour pressure deficit (VPD; dotted line). (a) Measurements on a cloudy day with low VPD (8 July 2009). Short time changes of P_p values during the daytime coincided with temporary fluctuations in solar radiation. (b) Measurements on a sunny day with high VPD (18 August 2009). Nocturnal hours are marked by grey columns.

balancing pressure (P_p) values indicating that both methods measure relative changes in leaf turgor pressure.

Diurnal stem and leaf water changes and their dependency on microclimate

Both, ΔW and P_p displayed distinct diurnal patterns which can be well explained by the daily course of stomatal regulation. Indeed, light-induced stomatal opening and closing control transpirational water loss which directly feeds back on leaf water status and through this on leaf turgor (Rüger 2008) and stem water content (Steppe *et al.* 2006; Turcotte *et al.* 2011). In the present study, this functional relationship is well demonstrated by the close correlation between the daily course of solar radiation (SR) and the diurnal pattern of ΔW and P_p . Further evidence for a pivotal role of varying sun light conditions and in turn, transpiration as driving force of temporal leaf water dynamics is given by the immediate P_p changes that occurred in response to short time fluctuations of SR. These changes are well within the reported range for reaction times of oak stomata to varying sun light conditions (Woods and Turner 1971), thus,

reflecting stomatal opening and closing in response to alternating sun light and shadow in the course of a day.

Interestingly, short time responses to varying sun light were not observed in stems, i.e. short time fluctuations of P_p displayed no feedback on ΔW , indicating that the hydraulic linkage between water-demanding leaves and the water-storing stem tissues is interfered by internal bottlenecks. Indeed, water storage in stems of woody plants occurs mainly in the elastic bark tissue where water can easily be withdrawn from living cells (Meinzer *et al.* 2001; Zweifel *et al.* 2001), thus, compensating for the daily transpirational water loss. Depletion of bark water storages, however, requires radial water flow from the bark to the water-conducting sap wood through symplastic pathways of the ray parenchyma (Tyree and Zimmermann 2002; Zimmermann *et al.* 2004), which may be limited by structural resistances, e.g. cell membranes, plasmodesmata and pits (Barnett 1982; Sauter and Kloth 1986; Van Bel 1990). Therefore, it is reasonable to assume that at short time scales, i.e. minutes to hours, leaf and bark water pools do not form a strictly coupled hydraulic system and this, in turn, might explain the lacking feedback of fast leaf turgor changes onto stem water storage. Circumstantial evidence for

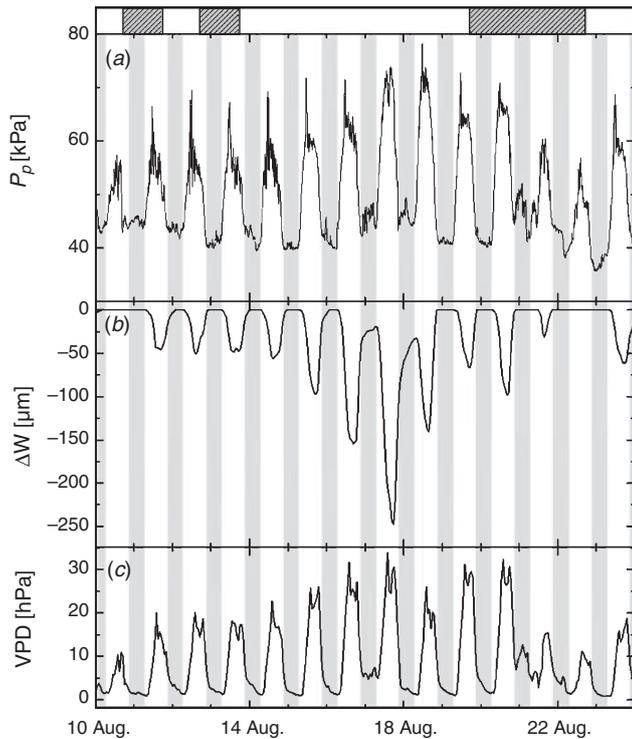


Fig. 4. Part of a long-term measurement of diurnal patterns of (a) P_p and (b) ΔW on a well-watered tree, together with (c) corresponding vapour pressure deficit (VPD). A high atmospheric water demand was recorded from 15 to 18 August 2009, resulting in an increase of the daily maximum values of P_p and the daily minimum values of ΔW respectively. Nocturnal hours are marked by grey columns. Irrigation events are marked by the filled rectangles above the panel.

this assumption is given by the time lags between daily negative peaking of ΔW and positive peaking of P_p , which point to a limited hydraulic linkage between bark and leaves, probably because of the flow resistance of the ray parenchyma pathway.

Long-term measurements on oaks with regular soil water supply revealed a distinct dependency of ΔW and P_p on daily weather conditions, particularly the change of the daily VPD. ΔW and P_p reached usually lower minimum and higher maximum peak values, respectively, on days with high VPD than on days with low VPD. This was especially the case for ΔW , which responded obviously more sensitive to day-to-day variations of VPD than P_p . This observation is in line with studies on other tree species showing high sensitivity of stem water content to VPD (Zweifel *et al.* 2005; Turcotte *et al.* 2011). It is likely that the higher sensitivity of the stem water content to VPD reflects a hierarchical order of water partitioning within trees giving more preference to water demanding leaves than to water-storing bark tissue to keep the leaf water content in an optimal range for physiological functions, e.g. photosynthetic carbon sequestration.

Responses of diurnal stem and leaf water changes to drought

Prolonged soil water shortage was reflected in the diurnal patterns of ΔW and P_p , with daily minimum and maximum values

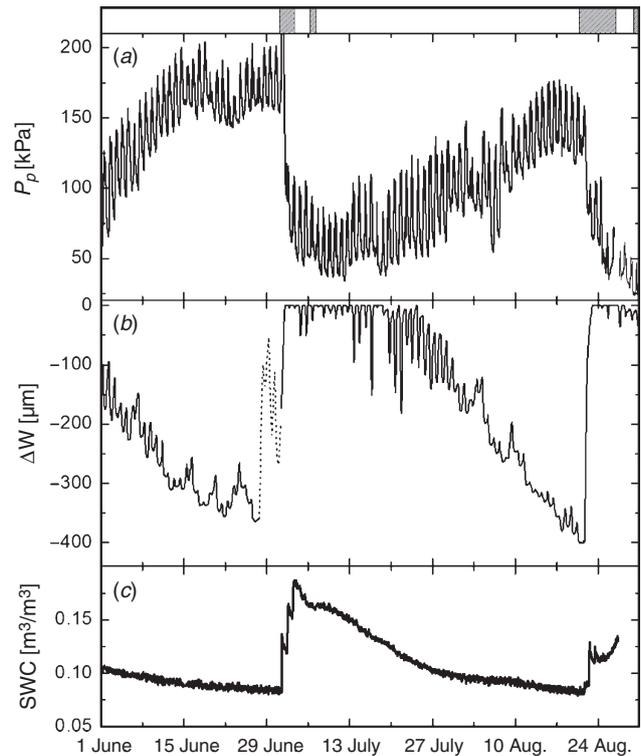


Fig. 5. Long-term measurements of diurnal patterns of (a) P_p and (b) ΔW together with (c) corresponding soil water content (SWC) at 62 cm depth. Measurements were performed on a tree subjected to two consecutive drought/re-watering cycles. Irrigation events are marked by the filled rectangles above the panel. Temporary ΔW recovery before first re-watering (dotted line) was caused by a heavy storm and rain event in the night from 28 to 29 June, moistening parts of the soil surface within the open top chambers (OTC) chamber and parts of the oak stem.

decreasing and increasing, respectively, with ongoing drought as well as incomplete night recovery indicating gradual water loss in stems and leaves. Further, with increasing drought, diurnal variations of ΔW were no longer observed, whereas those of P_p were maintained at a level of low turgor pressure. One explanation for this difference is that it is more difficult to withdraw water from the bark close to its depletion point (Zweifel *et al.* 2005) whereas diurnal leaf turgor variations proceed as long as daily transpirational water loss occurs. Indeed, under severe drought conditions oaks may maintain substantial transpiration rates, i.e. stomata open partly during the day, contrary to many other tree species that show earlier downregulation of leaf transpiration due to lower drought thresholds for stomatal closure (Abrams 1990; Zweifel *et al.* 2007, 2009).

Another result of this study shows that the time lags between daily negative peaking of ΔW and positive peaking of P_p increased from ~ 2 to 9 h with ongoing drought. This was mainly a result of the strongly delayed peaking times of ΔW , which may be indicative for a diminished feedback regulation of stem water content by the daily water demand of transpiring leaves. Increasing water flow resistances that limit the hydraulic connectivity of bark and leaves may contribute to this drought

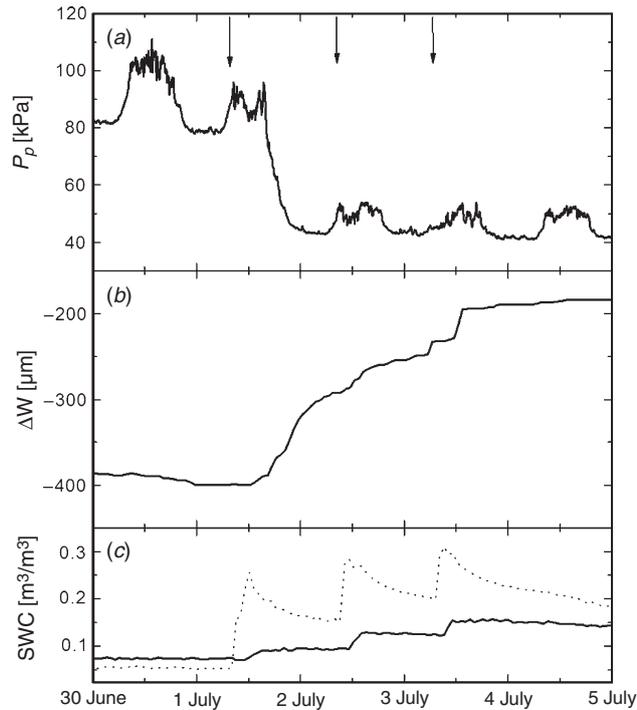


Fig. 6. Effect of re-watering on (a) P_p and (b) ΔW of a drought-subjected tree together with (c) corresponding soil water content (SWC) at 12 cm (dashed line) and 88 cm (solid line) depth. Stepwise re-watering was performed on 3 consecutive days (marked by arrows) starting on 1 July after long-term drought.

Table 1. Average response time in minutes of P_p and ΔW upon re-watering (mean \pm s.e.)

Parameter		P_p	ΔW
Re-watering I	First response	63 \pm 27 ($n=5$)	285 \pm 79 ($n=4$)
	Full recovery	1158 \pm 42 ($n=5$)	1920 \pm 551 ($n=4$)
Re-watering II	First response	40 \pm 24 ($n=7$)	130 \pm 20 ($n=3$)
	Full recovery	1882 \pm 443 ($n=7$)	2385 \pm 172 ($n=4$)

effect. Using a broad array of techniques Westhoff *et al.* (2009) have recently shown that the axial water pathways of the stem and the branches of tall trees became more and more interrupted by air with ongoing drought. Similarly, higher rates of xylem embolism and increasing discontinuity of the xylem conduits may have increased the time lag between ΔW and P_p peaking in our study. This is supported by a rough calculation of the water flow velocity between the dendrometer and the LPCP probe sites. On average, the distance between both sites was ~ 150 cm. Then, for an average delay time of 2 h between the daily peaking times of ΔW and P_p (as observed in well-watered trees) the water velocity in the xylem is calculated to be 0.21 mm s^{-1} . This value is of the order of the magnitude determined by flow-weighted NMR and other techniques on various plant species (e.g. Zimmermann 1983; Rokitta *et al.* 1999; Wistuba *et al.* 2000). In contrast, for an average delay time of 9 h between both parameters the xylem

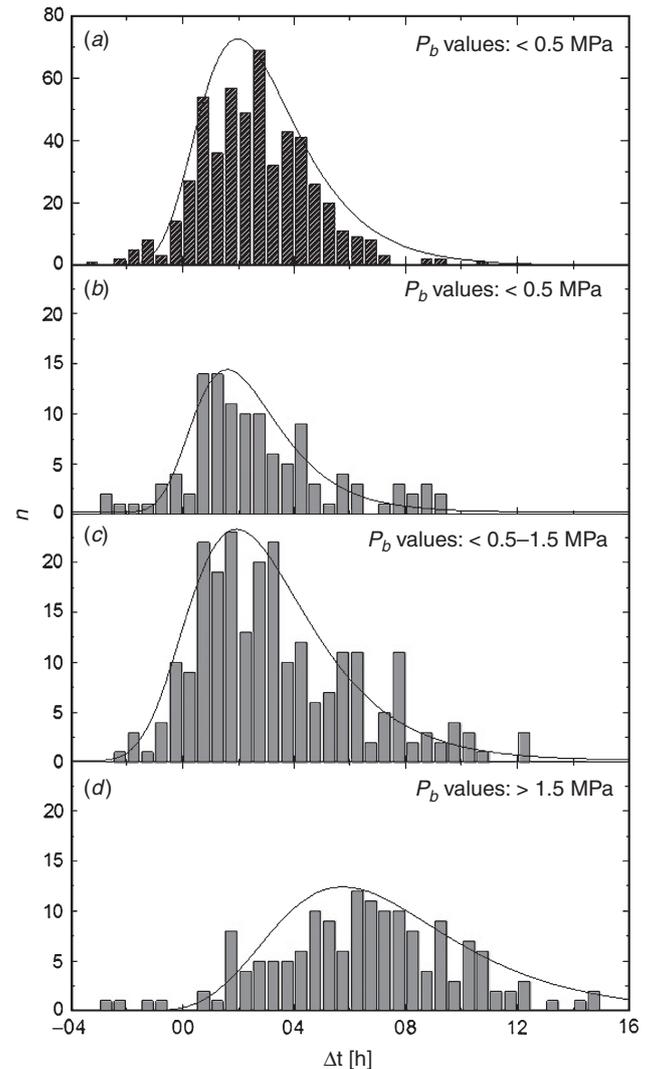


Fig. 7. Frequency distribution of the time difference (Δt) between daily ΔW and P_p peaking. (a) Well-watered trees (predawn P_b values: < 0.5 MPa). (b–d) Drought subjected trees at different stages of the drought treatment (predawn P_b values: < 0.5 MPa, 0.5 to 1.5 MPa, > 1.5 MPa).

water velocity is extremely small ($\sim 0.05 \text{ mm s}^{-1}$). This shows that concomitant measurements of ΔW and P_p using dendrometers and LPCP probes can give useful information about the velocity of water ascent in trees.

Conclusion

The present study demonstrates that automated dendrometers and the recently developed LPCP probe are user-friendly and continuously operating tools for studying tree water relations with great precision and high time resolution. Both techniques were applied to young oak trees allowing for concomitant measurements of water-related stem radius variations (ΔW) and turgor-dependent leaf patch pressures (P_p). Measurements performed over several months revealed not only the dependency of stem water content and leaf turgor on short and long-term

fluctuations of microclimate variables (solar radiation, atmospheric vapour pressure deficit) and soil moisture, but also provided insights into the hydraulic relationship between stem and leaves. The diurnal patterns of ΔW and P_p changes and the measured time lags between them provided some evidence that water storage in stems contribute to the water demand of transpiring leaves, thus, buffering temporal imbalances in transpirational water loss and soil water uptake. Knowledge of this hydraulic interaction may advance our understanding of tree water relations and may elucidate the mechanisms by which trees cope with temporal water shortage.

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