



Research paper

Stem water storage in five coexisting temperate broad-leaved tree species: significance, temporal dynamics and dependence on tree functional traits

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The functional role of internal water storage is increasingly well understood in tropical trees and conifers, while temperate broad-leaved trees have only rarely been studied. We examined the magnitude and dynamics of the use of stem water reserves for transpiration in five coexisting temperate broad-leaved trees with largely different morphology and physiology (genera *Fagus*, *Fraxinus*, *Tilia*, *Carpinus* and *Acer*). We expected that differences in water storage patterns would mostly reflect species differences in wood anatomy (ring vs. diffuse-porous) and wood density. Sap flux density was recorded synchronously at five positions along the root-to-branch flow path of mature trees (roots, three stem positions and branches) with high temporal resolution (2 min) and related to stem radius changes recorded with electronic point dendrometers. The daily amount of stored stem water withdrawn for transpiration was estimated by comparing the integrated flow at stem base and stem top. The temporal coincidence of flows at different positions and apparent time lags were examined by cross-correlation analysis. Our results confirm that internal water stores play an important role in the four diffuse-porous species with estimated 5–12 kg day⁻¹ being withdrawn on average in 25–28 m tall trees representing 10–22% of daily transpiration; in contrast, only 0.5–2.0 kg day⁻¹ was withdrawn in ring-porous *Fraxinus*. Wood density had a large influence on storage; sapwood area (diffuse- vs. ring-porous) may be another influential factor but its effect was not significant. Across the five species, the length of the time lag in flow at stem top and stem base was positively related to the size of stem storage. The stem stores were mostly exhausted when the soil matrix potential dropped below –0.1 MPa and daily mean vapor pressure deficit exceeded 3–5 hPa. We conclude that stem storage is an important factor improving the water balance of diffuse-porous temperate broad-leaved trees in moist periods, while it may be of low relevance in dry periods and in ring-porous species.

Keywords: *Acer pseudoplatanus*, *Carpinus betulus*, diffuse-porous, electronic dendrometers, *Fagus sylvatica*, *Fraxinus excelsior*, ring-porous, sap flux measurement, time lag of flow, *Tilia cordata*.

Introduction

The water status of plants is primarily determined by the water status of the soil and the atmosphere. However, plants have developed several mechanisms of internal water flux regulation that partially uncouple plant water status from atmospheric and soil hydrological control. These mechanisms are closely linked to morphological and physiological traits (Zweifel et al. 2002)

and thus vary with plant size, species and plant functional type. During the last three decades, much progress has been made in our understanding of plant internal water storage and hydraulic capacitance and their importance for daily and seasonal transpiration (e.g., Waring et al. 1979, Čermák et al. 1982, 1984, 2007, Schulze et al. 1985, Holbrook 1995, Goldstein et al. 1998, Phillips et al. 2003, Meinzer et al. 2004,

Scholz et al. 2007, 2008). It becomes increasingly evident that the water transpired by a tree during the day is not only extracted from the soil but that water stored in the roots, trunks, branches and leaves can also serve as transient or intermediate source for transpiration (Scholz et al. 2011). How important these internal sources are, depends on tree size, wood anatomy and sapwood dimensions (Schulze et al. 1985), and also on environmental conditions (Loustau et al. 1996). Despite this evidence, some authors concluded for a number of woody plants that the amount of transpired water originating from internal stores is not significant (Tyree and Yang 1990) or is only relevant in plants with inherently low transpiration rates (Holbrook 1995). Apart from this discussion on the quantitative importance of internal storage, it has been suggested that stored water in woody plants may play an important role by temporarily replacing water lost by transpiration, thereby transiently improving leaf water status which may enable the plant to maintain stomatal opening and carbon assimilation (Waring et al. 1979, Čermák et al. 1982, 1984, 2007, Goldstein et al. 1984, 1998, Borchert 1994, Phillips et al. 2003, Scholz et al. 2008).

In trees, stems and branches, as well as roots and leaves, can store water. Whether stored water may meet transpiration demands for considerable periods of time depends not only on the size of the storing compartments but also on the flow resistances between storage tissues and xylem (Waring and Running 1978). It is assumed that at least the initial water transpired in the crown after dawn is supplied in part from internal water stores. In large trees, withdrawal of stem water may cause a considerable apparent lag period between the fluctuation of transpiration and that of sap flow near the stem base (Andrade et al. 1998). Later in the afternoon, the storage will be replenished when stem sap flow typically exceeds water flow through the crown (Goldstein et al. 1998, Phillips et al. 2003). Consequently, one approach of estimating the amount of stored water in trees is to compare the integrated values of stem base and crown sap flow on a 24-h basis (Goldstein et al. 1998, Phillips et al. 2003, Meinzer et al. 2004).

Stored water in plants can be expressed as water storage capacity (amount of available water contained in a tissue or plant, with the unit kg) and hydraulic capacitance (C , i.e., the ratio of change in tissue water volume to change in its water potential, $C = \Delta W / \Delta \Psi$, with the unit kg MPa^{-1} , Phillips et al. 2009, Scholz et al. 2011). The focus of this paper is on water storage capacity and the daily use of stored water. Estimates of tree water storage as percentage of total daily transpiration vary over a broad range from <10 to over 50% (Waring et al. 1979, Goldstein et al. 1998, Phillips et al. 2003, Meinzer et al. 2004, Betsch et al. 2011), but normally do not exceed 30% of daily water use (Meinzer et al. 2008). It has been shown that the use of stored water for daily transpiration scales with tree trunk length and sapwood cross-sectional area, independent of

species (Goldstein et al. 1998, Phillips et al. 2003, Meinzer et al. 2004). Because wood density is a major determinant of hydraulic capacitance and both factors are inversely related, tree species with softer wood can store and utilize more water when transpiration requirements are high, than species with hard wood (Stratton et al. 2000, Meinzer et al. 2004, Pratt et al. 2007, Scholz et al. 2007). This indicates that the functional significance of water storage should differ not only between the major tree groups of conifers and broad-leaved trees (hardwoods), but also among tree species within these groups when their wood density, hydraulic architecture and strategies of water status regulation are markedly different. Species-rich temperate broad-leaved forests in Europe and eastern North America can harbor a remarkable functional diversity of tree species that differ with respect to wood density (<0.3 to >1 g cm^{-3}), wood anatomy (diffuse- vs. ring-porous trees and variable vessel dimensions), drought tolerance and isohydric or anisohydric behavior (Ewers et al. 2007, Taneda and Sperry 2008, Chave et al. 2009, Köcher et al. 2009, 2012a). However, only few studies have searched for differences in plant internal water storage among different temperate tree species (e.g., Čermák et al. 1982, Steppe and Lemeur 2007, Betsch et al. 2011); most studies on plant water storage concentrated on tropical and coniferous trees.

Water storage in trees and its fluctuation over time is associated with the reversible change in the radial dimensions of stems and branches, which reflect the use and refilling of the internal stores (Garnier and Berger 1986, Irvine and Grace 1997, Zweifel et al. 2001, Perämäki et al. 2005). For example, Scholz et al. (2008) could show the importance of outer parenchyma and sapwood tissues as storage compartments in six woody species of the Brazilian savanna; both tissues accounted for 16–31% of the transpired water during the day. These authors also demonstrated the importance of seasonal change for internal water storage. During the wet season, the store was regularly fully replenished and stem diameter recovered overnight. In contrast, during the dry period, a gradual decline in the stem's daily maximum diameter occurred over several consecutive days, indicating incomplete overnight rehydration. Thus, stem radial changes may serve as an indicator for diurnal and seasonal dynamics of the utilization and recharge of stored water and also for current plant water status.

The objective of this study was to examine the magnitude and dynamics of the use of stem water reserves in five coexisting temperate broad-leaved trees with largely different morphology and physiology (genera *Fagus*, *Fraxinus*, *Tilia*, *Carpinus* and *Acer*). These tree species are common and widespread in Central Europe and known to differ in drought sensitivity (insensitive to moderately sensitive), xylem anatomy (diffuse- vs. ring-porous), type of mycorrhiza (ecto vs. arbuscular) and successional status (early/mid- to late-successional) (Hölscher

et al. 2002, Köcher et al. 2009, Ellenberg and Leuschner 2010). With wood densities ranging from 0.43 (*Tilia*) to 0.67 g cm⁻³ (*Carpinus*), this species sample covers a large part of the variation in wood density found in temperate broad-leaved trees (Chave et al. 2009). Sap flux density was recorded synchronously at five positions along the root-to-branch flow path of mature trees (roots, three stem positions and branches) with high temporal resolution (2 min) and related to diurnal stem radius fluctuations monitored with electronic point dendrometers. By selecting mature trees of roughly similar size (25–28 m tall) and diameter at breast height (DBH, 35–50 cm) that grew in close neighborhood to each other in a mixed stand and occupied similar positions in the canopy, we minimized the influence of tree size and of variable environmental conditions on internal water storage (Scholz et al. 2011). We thus expected that differences in water storage patterns should mostly reflect species differences in wood anatomy, hydraulic architecture or other traits. We hypothesized that (i) in diffuse-porous species, the amount of stored water used for transpiration decreases with increasing wood density, (ii) ring-porous *Fraxinus* uses smaller amounts than all investigated diffuse-porous species due to its small sapwood area, (iii) the amount of stored water used for daily transpiration decreases with decreasing soil water availability and increasing stem water deficit (SWD), (iv) sap flux density fluctuations observed in sunlit upper canopy branches are registered in the stem top, stem base and finally the roots with increasing apparent time lags and (v) species with a greater use of stored water show larger time lags between stem top and stem base flow peaks.

Materials and methods

Study site and tree species

The study was conducted in summer 2009 in a species-rich temperate broad-leaved forest in Hainich National Park in western Thuringia, Central Germany (51°04'N, 10°30'E), where five or more tree species of the genera *Fagus*, *Tilia*, *Carpinus*, *Fraxinus* and *Acer* are co-occurring. The mixed forests are

mostly belonging to the Stellario-Carpinetum community (oak–hornbeam forests).

Luvisol is the dominant soil type, which developed from loess and which covers Triassic limestone as bedrock (Guckland et al. 2009). The mean annual temperature of the site is 7.5 °C, the mean annual precipitation is 590 mm (1973–2004, Deutscher Wetterdienst, 2005). Mean tree height varies between 27.9 m in the denser part of the forest (614 stems ha⁻¹) and 32.9 m in the less dense forest area (392 stems ha⁻¹) (Gebauer et al. 2008). The average stand age of the canopy trees varies between 90 and 120 years (Schmidt et al. 2009).

The present study was conducted with the five most abundant broad-leaved tree species of the Hainich forest, i.e., sycamore maple (*Acer pseudoplatanus* L.), European beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.), European hornbeam (*Carpinus betulus* L.) and little-leaf linden (*Tilia cordata* Mill.) that differ considerably in functional traits (Table 1). The species represent either early- to mid-successional, or mid- to late- and late-successional trees with contrasting light requirements and canopy transmissivity, and they vary in terms of hydraulic properties, drought tolerance and type of mycorrhiza. Two individuals per species (*Acer*: one) with stand-representative height and stem diameters were selected for continuous xylem sap flux and stem radius monitoring. All trees were mature dominant individuals reaching into the upper canopy (height 25.0–28.3 m) located in the stand at a maximum distance of 50 m from each other. We used a mobile canopy lift (model DL30, Denka-Lift AS, Denmark) with a maximum height of 30 m to access the upper stem and the sun canopy branches.

Hydrological and microclimatological measurements

Volumetric soil water content (Θ , in m³ m⁻³) was measured twice per day in a soil profile at a short distance (<50 m) from the group of the nine measurement trees using time domain reflectometry probes (CS616 Water Content Reflectometer, Campbell Scientific, Cambridge, UK) installed at three soil depths (10, 30 and 50 cm). The soil moisture data were used

Table 1. Morphological and functional traits of the five studied tree species according to the categorization of species properties in Bartels (1993), Hölscher et al. (2002), Gebauer et al. (2008), Köcher et al. (2009) and Ellenberg and Leuschner (2010).

	<i>F. excelsior</i>	<i>A. pseudoplatanus</i>	<i>C. betulus</i>	<i>T. cordata</i>	<i>F. sylvatica</i>
Family	Oleaceae	Aceraceae	Betulaceae	Tiliaceae	Fagaceae
Successional status	Early/mid	Mid/late	Mid/late	Mid/late	Late
Shade intensity ¹	3	4	4	4	5
Drought tolerance	High	Mid/low	Mid	Mid	Low
Type of mycorrhiza ²	AM	AM	ECM	ECM	ECM
Xylem anatomy ³	Ring	Diffuse	Diffuse	Diffuse	Diffuse
Wood density ⁴ (g cm ⁻³)	0.59 (0.045) a	0.59 (0.030) a	0.67 (0.024) b	0.43 (0.063) c	0.65 (0.025) b

¹Relative assessment of shade intensity below mature trees (3—moderate, 4—high, 5—very high).

²AM, vesicular-arbuscular mycorrhiza; ECM, ectomycorrhiza.

³Ring-porous, diffuse-porous.

⁴Data from Gebauer et al. (2008), different letters indicate significant differences between species in wood density.

to estimate soil matrix potential (Ψ_s) for a soil depth of 10 cm using the program Rosetta Version 1.2 (Schaap et al. 1998) with the required soil physical parameters (clay content and bulk density) being taken from the soil analyses of Guckland et al. (2009) in the Hainich forest.

Relative air humidity and air temperature were recorded continuously in the upper canopy at ~25 m height in the tree *Fagus* #2 using a Rotronic temperature and humidity probe (MP100A Hygromer, Rotronic, Ettlingen, Germany). Measurements were taken every 30 s and stored as 2- and 30-min averages with a Campbell CR1000 data-logger (Campbell Scientific) and used to calculate the vapor pressure deficit (VPD). Precipitation was recorded hourly at the nearby (2 km) Weberstedt/Hainich meteorological station (Meteomedia GmbH). Incoming short-wave radiation was recorded with a pyranometer (Campbell CS300, Campbell Scientific) at 2- and 10-min resolution, installed on a 45-m-high tower about 2 km distant to the study site. All diurnal measurements are based on solar time which is 80 min behind Central European Summer Time.

Sap flux measurements

In the nine trees from five species, sap flux density was measured simultaneously at five different positions of the root-to-leaf flow path of the trees during the period 15 August to 13 September 2009, using two different flux measurement approaches. Roots and sunlit upper canopy branches of ~10 mm in diameter (range: 9–14 mm) were equipped with miniature sap flow gauges, which measure sap flow rates by means of the constant power heat-balance method with external heating of root and branch segments according to Sakuratani (1981), Senock and Leuschner (1999) and Coners and Leuschner (2002). The sap flux density in stem xylem was recorded at three positions on the stem with Granier-type heat-dissipation probes (Granier 1987), i.e., at the stem base (ca. 10 cm above ground), at breast height (1.3 m height) and at the stem top (ca. 1 m below the insertion of the main canopy branches). The height of the sensor at the stem top (crown base) differed considerably between the trees ranging from 5.5 to 16.2 m (Table 3).

The self-manufactured miniature sap flow gauges consisted of two pairs of thermocouples and a thermopile embedded in a flexible cork-neoprene jacket that ensured good contact to the root or branch surface. A Kapton film resistance heater (Heater Designs Inc., Bloomington, CA, USA) was placed between the thermocouple junctions and supplied with a constant power of 0.04–0.07 W to heat the segment. The axial dissipation of heat was monitored by the thermocouples and the radial by the thermopile. From these fluxes and the known energy input, the heat balance of the system is solved for the amount of heat transported with flowing water in axial direction (for details see Coners and Leuschner 2002). The heat flow (in J h^{-1} per segment) is then converted with the gauge

heat conductance (K_g) and the heat capacity of water ($4187 \text{ J kg}^{-1} \text{ K}^{-1}$) to mass flow rates (in g h^{-1}). K_g was recalculated daily at conditions of zero flow which was assumed to occur before dawn. These calculations were performed with a graphical interactive software tool developed by H. Coners (unpublished data).

Each tree was equipped with four miniature gauges, two mounted on roots and two on canopy branches. The gauges were insulated with thick layers of polyurethane foam that was fixed with a metal clip. For installing the root gauges, we dug small soil pits in the stem vicinity to search for suitable 10-mm roots with straight and non-branched morphology. By tracing the roots back to a major root, the species identity was ensured. Roots suitable for measurement were found mostly in 5–20-cm soil depth. After gauge installation, the small soil pits were covered with wooden plates to minimize thermal gradients and prevent disturbance. The gauges were mounted in a similar manner on sunlit upper canopy branches using the lifter for access, but the gauges were additionally insulated with polyurethane tubes, wrapped around the gauge and branch and enclosed in a reflecting aluminum foil to minimize thermal gradients across the measuring point.

Granier-type sensors were mounted at the stem base, breast height and stem top (crown base) to monitor sap flux density in the outer 20 mm of the stem xylem. The Granier system consisted of two probes inserted into the wood ca. 15 cm apart axially. We used 20-mm-long probes for all trees except for the ring-porous *Fraxinus* trees, which were equipped with shorter (10 mm long) probes to account for the smaller sapwood depth in this species. The upper probe was constantly heated with a power of 200 mW, while the lower one served for monitoring the reference temperature of the stem. The temperature difference between the heated and the reference probe was recorded continuously and related to the daily maximum temperature difference observed at predawn when minimum or no flow occurred. Sap flux density (J_s , in $\text{g m}^{-2} \text{ s}^{-1}$, see Table A1 in the Appendix) was calculated according to the empirical equation given by Granier (1987). All 27 stem sensors were insulated with polystyrene mats to keep off stem runoff and to minimize measuring errors due to external thermal gradients.

The sensor signals from the Granier-type sensors and the miniature gauges were recorded every 30 s and stored as 2- and 30-min averages with a CR1000 data-logger (Campbell Scientific). Owing to a technical problem, we were able to collect data with a resolution of 2 min only for the period from 28 August to 13 September 2009.

Recording of stem radius variation and calculation of tree water deficit

All nine trees were equipped with spring-loaded linear displacement potentiometers (model MMR 10_11 R5K, MEGATRON

Elektronik, Munich, Germany) with a resolution of $<10\ \mu\text{m}$ to detect diurnal and seasonal stem radius fluctuations. The potentiometers were mounted in the center of stainless-steel frames and then fixed to the stem at 1.3 m height with two screws anchored at least 5 cm deep into the xylem and 6 cm apart from the measuring section. The potentiometers were placed with their tips onto the bark, which had been previously smoothed, and covered and shielded with a reflecting foil. Changes in stem radius were measured every 30 s and logged as 30-min averages using a CR1000 data-logger (Campbell Scientific).

To distinguish between growth-related and water-status-related changes in stem radius, we applied a de-trending approach according to Zweifel et al. (2005) and Drew et al. (2011). This procedure yielded a growth-independent estimate of stem radius change as caused by water volume change in the stem wood due to water loss or addition. By relating the measured stem radius to an assumed maximal radius under fully hydrated conditions at the time of measurement (and with account for growth-related radius changes), we expressed the radius data as the difference between actual and respective maximal radius in μm (termed hereafter 'apparent stem water deficit', SWD, because all values are negative). Daily minima of SWD (SWD_{min} , i.e., smallest deviation from maximal radius) are typically observed in the early morning hours when refilling of the trunk water store is at its maximum. We also calculated the magnitude of daily stem radius shrinkage (SRS, in μm), defined as the difference (diurnal amplitude) between the morning maximum and daily minimum of stem radius.

Calculation of stem water storage

For estimating the extraction of stored stem water during a day, we calculated the difference between the sap flow rates at the stem base and stem top of a tree ($J_{r\ \text{stembase}} - J_{r\ \text{stemtop}}$, both flows expressed in $\text{kg h}^{-1}\ \text{tree}^{-1}$) and integrated the difference over the whole day (from midnight to midnight on the next day, Figure 3). In this calculation, we first extrapolated the sap flux density data measured at breast height (J_s , in $\text{g m}^{-2}\ \text{s}^{-1}$, recorded at 30-min resolution) to daily water consumption rates (J_{rd} , $\text{kg day}^{-1}\ \text{tree}^{-1}$) by using empirical data on the radial sap flux density profile in the five species from Gebauer et al. (2008); this source includes the calculation of the hydroactive sapwood area with species-specific power functions. Second, the information on diurnal sap flux patterns at the stem base or stem top were incorporated into the daily flow totals by dividing every half-hourly J_s value of a given day by the respective daily J_s total at stem base or top, yielding half-hourly flows as a fraction of daily flow. These fractional flow rates were subsequently multiplied by the daily flow total calculated for the stem at breast height assuming that the stem store is completely refilled overnight and total daily flow at base and top are thus equal. Half-hourly flows into (positive values, refilling) or out of the stem store (negative values, withdrawal) were then

obtained by calculating the difference in flow rate between stem base and top over the day. Adding up all negative values over a day gives an estimate of the daily use of stored stem water (S_d , in $\text{kg day}^{-1}\ \text{tree}^{-1}$). The daily use of stored stem water was further expressed in percent of the tree's daily total water use ($S_{d\ \text{relative}}$) and in relation to bole volume (as calculated from the stem dimensions between stem base and top, $S_{d\ \text{bole}}$, in $\text{kg m}^{-3}\ \text{day}^{-1}$).

The procedure described assumes complete refilling of the stem store by dawn which, however, may not occur every night. Our dendrometer data indicate the development of longer-lasting SWDs in most of the trees. In several cases, the deficits persisted until the end of the study period when plenty of rain refilled the store (see Figures 1c and 7). Therefore, we extended the daily approach to a measuring period of 24 days (21 August–13 September 2009), assuming equality of water inflow and outflow only at the end of this period. In this case, we multiplied the half-hourly fractional flows (in this approach calculated in relation to the entire 24-day period) by the total water consumption in this period, thus taking possible lag phases in the refilling of the stem water store into account. As a consequence, the calculated daily flows into and out of the store did not necessarily match at the end of a day, and the consecutive days showed either positive (refilling) or negative (loss) daily totals of water exchange with the store. The ratio of the daily sap flow rate at the stem base and the stem top ($J_{rd\ \text{stembase}\ 24\text{-day}}/J_{rd\ \text{stemtop}\ 24\text{-day}}$), calculated in the 24-day analysis, expresses whether water is added to (ratio >1) or withdrawn from (ratio <1) the store during a day.

Data analysis

Basic statistics (arithmetic means and standard errors) were calculated with Microsoft Office Excel 2003 software. Regression analyses were conducted with the program Xact 7.20g (SciLab GmbH, Hamburg, Germany). Cross-correlation analyses for determining apparent time lags in sap flux density between different measuring points along the flow path (root-to-branch) were conducted with SAS software, version 9.1 (SAS Institute Inc., Cary, NC, USA) using the arima procedure. Sap flux density time series with 2-min resolution from the different measuring positions for the period from 28 August to 13 September 2009, normalized by the daily flux density maximum (J_{sn}), were shifted along the time axis until the highest coefficient of determination with respect to congruency in temporal flux density variation was found among the curves.

Results

Microclimatic conditions and soil moisture status in the measuring period

While the study year 2009 was relatively warm ($8.7\ ^\circ\text{C}$) and wet (774 mm) compared with the long-term averages

(7.5 °C and 590 mm), the study period in the second half of the growing season (15 August to 13 September) was the driest of the whole vegetation period with soil matrix potentials at 10 cm soil depth continuously decreasing to a minimum of -0.14 MPa (Figure 1c). Daily mean air temperature (T_{mean}) varied between 9.2 and 23.7 °C and the VPD reached values of almost 30 hPa on the 20th of August, which was the warmest day of the year (Figure 1a). Mean daily relative humidity (RH_{mean}) ranged between 56 and 91% and total daily global radiation (I_{tot}) varied between 7 and 23 MJ m⁻² day⁻¹ (Figure 1b).

Variation of sap flux density with species and along the root-to-branch flow path

Xylem sap flux density (J_s , g m⁻² s⁻¹) showed a considerable variation among the five coexisting tree species for a given measuring position and also between the five measuring positions (sunlit canopy branch, stem top, stem at breast height, stem base and root) of a tree (Figure 2). Calculated as mean daily sap flux density (J_{sd} , g cm⁻² day⁻¹), the *Tilia* trees showed the highest mean J_{sd} values at DBH (1.3 m) height (90 g cm⁻² day⁻¹), the *Acer* and *Fraxinus* trees the lowest figures (54 and 57 g cm⁻² day⁻¹) and *Fagus* and *Carpinus* had intermediate values (78 and 70 g cm⁻² day⁻¹), even though tree height and DBH were comparable among the species. In general, the daily means of sap flux density (J_{sd}) increased in

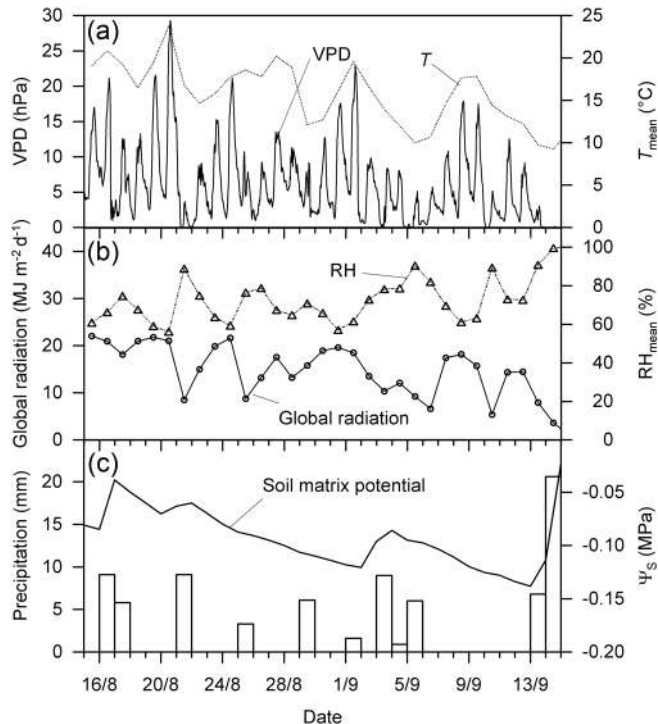


Figure 1. Seasonal course of (a) daily mean air temperature (T_{mean}) and half-hourly values of VPD, (b) mean daily relative air humidity (RH_{mean}) and daily totals of global radiation (I_{tot}) and (c) daily precipitation (P) and soil matrix potential (Ψ_s) at 10 cm soil depth from 15 August to 15 September 2009, in the Hainich forest.

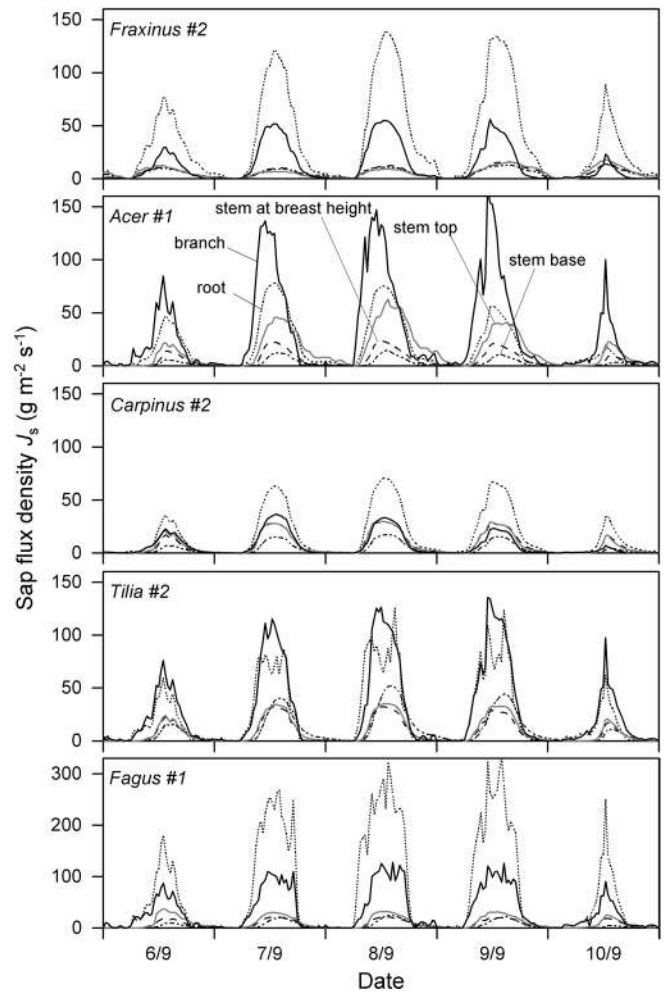


Figure 2. Course of sap flux density (J_s , g m⁻² s⁻¹) in tree organs over a period of 5 days (resolution 30 min) in September 2009. For every species one individual is shown. Note different scale of the y-axis in *Fagus* tree #1.

all species from the stem base to the top. However, much higher sap flux densities than in the stem were recorded in roots (~ 10 mm in diameter) and sunlit canopy branches (typically 2–4 times larger values) with peak flux densities of 1707 g cm⁻² day⁻¹ measured in a *Fagus* root and of 894 g cm⁻² day⁻¹ recorded in a branch of a *Carpinus* tree. Except for *Acer*, the mean J_{sd} values were generally higher in the roots than in the branches of similar diameter (Figure 2). The ratio of root-to-branch flux density ranged from 0.51 in *Acer* to 1.25, 1.67 and 1.83 in *Carpinus*, *Fagus* and *Fraxinus*, respectively and peaked with 2.07 in *Tilia*.

The temporal variation of flux density showed very similar and mostly congruent patterns in the branches, stems and roots of the same tree as is visible in the normalized flux data (J_{sn}) with high temporal resolution (2 min) (Figure 3), which showed a close correlation to the fluctuation in VPD (correlation data not shown). However, we could detect distinct time lags in flow patterns between branches, stem and roots in a

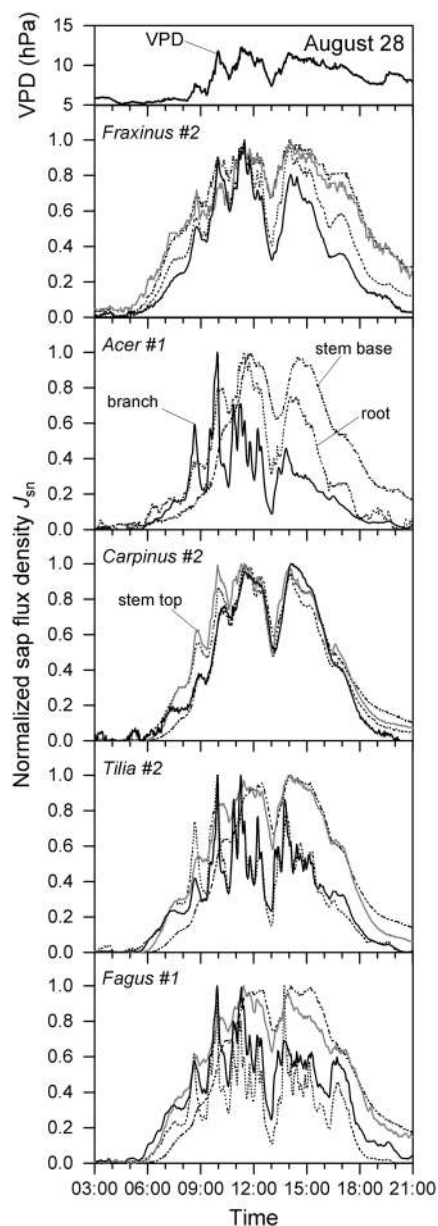


Figure 3. Sap flux density on 28 August 2009, normalized to daily peak flow (J_{sn}) in sun-canopy branches, stem top, stem base and roots of each one tree of the five species (2-min resolution). Data of branches and roots are means of two sensors each. The diurnal course of VPD at canopy height is depicted in the top panel.

tree as they became visible when high-resolution flux density time series from different measuring positions in the tree were shifted along the time axis until the highest degree of correlation was achieved (Table 2). In nearly all investigated trees, largest time lags between flux density patterns were observed between branch and stem base (>1 h in four of the nine trees), followed by considerable time lags also between stem top and stem base and between sunlit canopy branches and stem top (often 20–50 min, Table 2). The largest single time lag was measured for the branch–stem base difference in *Acer* tree #1 (116 min). Surprisingly, we found only negligible time lags

between branch and root sap flux densities in most of the trees (except for *Acer*) and root sap flux preceded stem sap flux in nearly all cases. Our results also indicate distinct species differences in the length of the time lag between peak fluxes; the ring-porous *Fraxinus* trees exhibited only minor time lags between different measuring positions (maximum delay of 4 min) and the time lags in *Fagus* tree #2 were also small, while much larger time lags were found in the other *Fagus* tree (#1) and in *Acer* tree #1.

Daily water use and the contribution of stored stem water

The daily water use (J_{rd} , kg day^{-1}) of the nine studied trees as extrapolated from sap flux measurements at breast height and flux density depth profiles ranged from 9 to 70 kg day^{-1} in its daily average (Table 3) with particularly small J_{rd} means (9 and 13 kg day^{-1}) being recorded in the ring-porous *Fraxinus* trees. Time series analysis of the diurnal course of sap flow at stem base and top ($J_{r \text{ stembase}}$ and $J_{r \text{ stemtop}}$) revealed a dynamic shift between phases of discharge and refilling of the stem water reservoirs (Figure 4). Water was usually withdrawn from stem storage during the morning hours and subsequently replaced in the afternoon and into the night as one would expect. However, in some species (e.g., tree #1 of *Acer*), we observed a more variable diel flow pattern with only a short time of water withdrawal in the morning, inflow of water into the storage around midday during maximum transpiration and water withdrawal again in the evening (Figure 4: second row).

The average amount of stored stem water that was used per day for transpiration (S_d) ranged from 0.5 kg day^{-1} in *Fraxinus* tree #2 to 11.9 kg day^{-1} in *Tilia* #1 (Table 3). Trees with a higher mean daily water consumption used a higher amount of stored water (positive relation, $R^2 = 0.62$, $P = 0.011$). The water withdrawn from stem storage accounted on average for 5.3 (*Fraxinus*) to 22% (*Acer*) of the trees' total daily transpiration. The species contrast was even more pronounced when the daily use of stored water was related to the stem volume relevant for storage (between stem base and stem top, Table 3), with highest values of withdrawal per volume found in the *Tilia* trees (4.18 and 6.99 $\text{kg m}^{-3} \text{ day}^{-1}$) and lowest in the *Fraxinus* trees (0.12 and 0.38 $\text{kg m}^{-3} \text{ day}^{-1}$), while *Acer*, *Carpinus* and *Fagus* showed intermediate values in the range of 1.44–3.09 $\text{kg m}^{-3} \text{ day}^{-1}$.

As expected, both daily water use (J_{rd}) and the daily use of stored stem water (S_d) were positively related to mean daily VPD, but the slope of the J_{rd} –VPD relationship was much steeper than that of the S_d –VPD relationship (Figure 5). Thus, the S_d/J_{rd} ratio tended to be higher on days with low evaporative demand.

When relating the mean daily use of stored water (S_d) of the four diffuse-porous species to the species' wood density, we found a significant negative relation ($R^2 = 0.98$, $P < 0.01$, Figure 6a). *Fraxinus* was not included in this analysis owing to

Table 2. Time lags between normalized peak sap flux densities (J_{sn}) of sunlit canopy branches, stem top, stem base and roots of the nine study trees calculated for a time series of up to 24 measuring days in the period from 21 August to 13 September 2009. Sap flux data with a resolution of 2 min were used which were normalized to the daily flux peak before cross-correlation analysis. Positive time lags indicate a delay of sap flux at the lower location in the tree compared to the upper location and vice versa.

Tree	Time lag between sensor locations (min)					
	br → st	br → sb	br → ro	st → sb	st → ro	sb → ro
<i>Fraxinus</i> #1	–	2	0	–	–	–2
<i>Fraxinus</i> #2	2	4	0	4	2	–2
<i>Acer</i> #1	68	116	58	36	–20	–52
<i>Carpinus</i> #1	32	82	0	28	–12	–40
<i>Carpinus</i> #2	2	24	2	24	–2	–28
<i>Tilia</i> #1	–8	24	8	44	8	–18
<i>Tilia</i> #2	28	86	0	40	–72	–128
<i>Fagus</i> #1	26	84	0	48	–38	–96
<i>Fagus</i> #2	–8	–8	–2	4	2	0

br, branch; st, stem top; sb, stem base; ro, root; –, missing data.

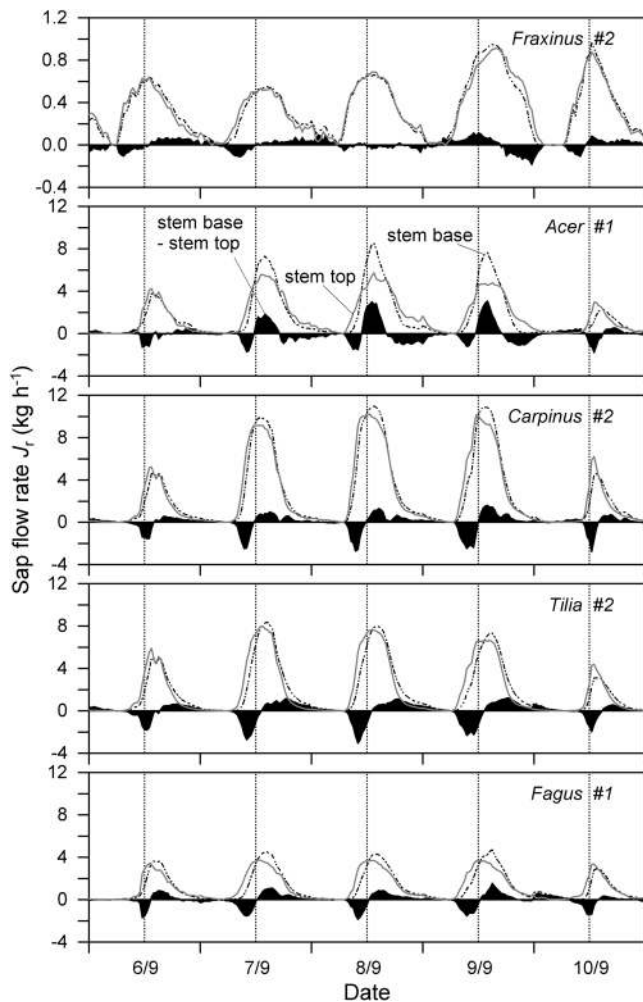


Figure 4. Diurnal course of sap flow rate (J_s , $\text{kg h}^{-1} \text{ tree}^{-1}$) at stem top (grey line) and stem base (dotted line) and time course of water withdrawal and refilling of stem reservoir (filled black area) on 5 days in September 2009 calculated as the difference between the two flows for one tree of each of the five species. Negative values indicate withdrawal of stored water and positive refilling. The thin vertical lines mark 1200 h. Note different scale of the y-axis in *F. excelsior* #2.

its small sapwood area. The relationship between S_d and sapwood area across the five species was not significant ($R^2 = 0.43$, $P < 0.23$, data not shown).

Species that used smaller daily amounts of stored water showed on average smaller apparent time lags between stem top and stem base flows than species with a larger S_d (significant positive relation across the five species, $R^2 = 0.95$, $P < 0.01$, Figure 6b).

Stem radius fluctuation, apparent SWDs and seasonal change in stem water storage

During the 4-week study period in late summer 2009, we observed in all trees the development of an apparent SWD, i.e., an increasing negative deviation of measured stem radius from the radius at full water saturation (Figure 7). The negative radius deviation was especially large in those trees which had stopped radial growth in this period as was found for the trees *Fraxinus* #2, *Acer* #1, *Carpinus* #1 and *Tilia* #2 (growth data not shown). Stem water deficit reached values of -50 to $-200 \mu\text{m}$ in certain trees at the end of August 2009, when the soil was relatively dry, but rapidly relaxed towards the zero line with the occurrence of rainfall around 5 September (Figure 1c). The daily minimum deviation of actual stem radius from the radius at fully hydrated conditions (SWD_{min} , typically measured in the early morning) showed for all trees (except for *Acer* #1) a strong exponential increase with a drop in the soil matrix potential (Ψ_s) at 10 cm soil depth (Figure 8). In the trees which showed radial growth in this dry period (*Fraxinus* #1, *Carpinus* #2, *Tilia* #1 and both *Fagus* trees), SWD_{min} started to rise rapidly beyond a Ψ_s threshold of approximately -0.1 MPa , whereas the other trees showed increasing SWD_{min} figures (negative values) already at higher (less negative) soil matrix potentials (Figure 8).

Daily SRS (or the diurnal stem radius amplitude) was, in contrast to SWD_{min} , more closely related to the evaporative demand

Table 3. Biometric data and parameters characterizing the use of stored water in the study trees. Sapwood area was calculated with power functions taken from Gebauer et al. (2008). The bole volume refers to the volume between the flux sensors at stem top and stem base and was calculated using Smalian's equation for volume estimation of logs. J_{rd} —mean daily water use per tree (kg day^{-1}), S_d —mean daily amount of stored stem water extracted, either expressed as daily total (kg day^{-1}), in percent of total daily tree water use (%) or related to bole volume ($\text{kg m}^{-3} \text{day}^{-1}$). Given are means \pm SE. J_{rd} averages were calculated from daily values of the period from 15 August–13 September 2009 ($n = 30$ days). Owing to missing data in stem base or stem top sap flux, the number of days (n) used to calculate averages of S_d varies between tree individuals.

Tree	DBH (cm)	Tree height (m)	Sapwood area (m^2)	Height of sensor at stem top (m)	Bole volume (m^3)	J_{rd} (kg day^{-1})	S_d (kg day^{-1})	$S_{d \text{ relative}}$ (%)	$S_{d \text{ bole}}$ ($\text{kg m}^{-3} \text{day}^{-1}$)	(n)
<i>Fraxinus</i> #1	41.16	28.05	0.0267	16.22	5.20	13.3 \pm 0.54	1.99 \pm 0.14	14.5 \pm 0.7	0.38 \pm 0.03	18
<i>Fraxinus</i> #2	36.96	27.5	0.0200	14.15	4.00	9.0 \pm 0.44	0.47 \pm 0.06	5.3 \pm 0.5	0.12 \pm 0.01	26
<i>Acer</i> #1	38.3	26.8	0.0981	13.88	4.22	45.4 \pm 3.12	6.64 \pm 0.72	22.0 \pm 3.7	1.57 \pm 0.17	12
<i>Carpinus</i> #1	36.41	24.95	0.0691	11.73	3.20	44.0 \pm 3.38	4.94 \pm 0.51	13.0 \pm 0.9	1.54 \pm 0.16	22
<i>Carpinus</i> #2	45.95	26.9	0.1139	5.72	1.82	70.5 \pm 5.05	5.60 \pm 0.28	10.5 \pm 1.1	3.09 \pm 0.15	24
<i>Tilia</i> #1	41.25	28.25	0.0876	6.07	1.70	65.1 \pm 4.49	11.91 \pm 0.84	18.8 \pm 0.7	6.99 \pm 0.49	30
<i>Tilia</i> #2	43.31	24.25	0.0945	5.52	1.61	55.5 \pm 3.51	6.72 \pm 0.38	14.2 \pm 0.8	4.18 \pm 0.24	24
<i>Fagus</i> #1	40.84	28.2	0.0954	11.35	3.53	32.0 \pm 1.65	5.09 \pm 0.28	16.6 \pm 1.0	1.44 \pm 0.08	28
<i>Fagus</i> #2	50.36	28.15	0.1425	8.83	3.25	54.1 \pm 3.99	4.86 \pm 0.34	9.6 \pm 0.5	1.50 \pm 0.10	30

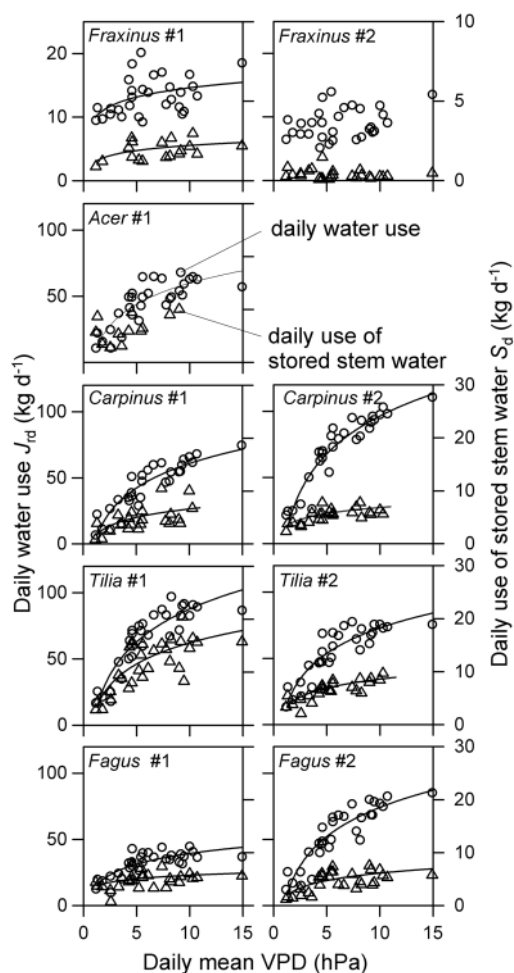


Figure 5. Daily water use (J_{rd} , kg day^{-1}) and daily use of stored stem water (S_d , kg day^{-1}) for the studied trees as a function of mean daily VPD. For trees with a significant relationship ($P < 0.05$), logarithmic functions of the type $y = a + b \times \ln(\text{VPD})$ are drawn. Note different scales of the y-axes in the *Fraxinus* trees.

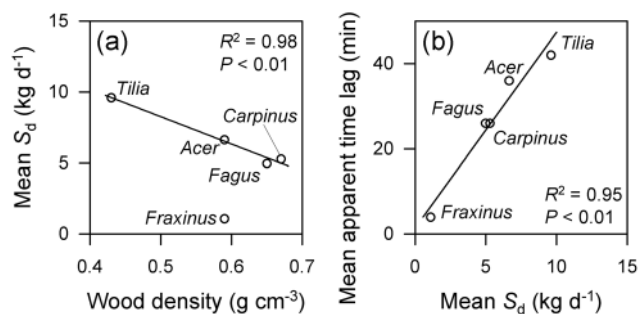


Figure 6. (a) Mean daily use of stored water (S_d , kg day^{-1}) per tree species in relation to the wood density of the five tree species. A linear regression line is drawn only across the four diffuse-porous species (excluding *Fraxinus*). (b) Mean time lag between sap flows at stem top and stem base as a function of mean daily use of stored water (S_d) across the five tree species.

showing an increase with increasing daily mean VPD. The dependence of SRS on VPD was best described by logarithmic functions (except for the *Fraxinus* trees: linear functions; data not shown). Accordingly, the SRS maxima occurred on days with high evaporative demand (20 August 2009 and 1 September 2009) with radius amplitudes as large as 245 and 116 μm in the trees *Fraxinus* #1 and #2, respectively, and of 75 μm in the *Tilia* trees, 62 μm in *Acer* #1, 44 and 81 μm in *Carpinus* #1 and #2, respectively, and of about 45 μm in the *Fagus* trees (Figure 7). In contrast to the maxima, the average SRS values for the study period differed only little between the tree species (range: 26.0–36.5 μm); an exception were the *Fraxinus* trees with a larger mean radius amplitude (80.6 μm).

Extraction (withdrawal and negative water flow) or addition of water to stem storage (recharge and positive flows) on a given day depended partly on the daily mean VPD. In five of the nine studied trees, the net daily recharge increased and the

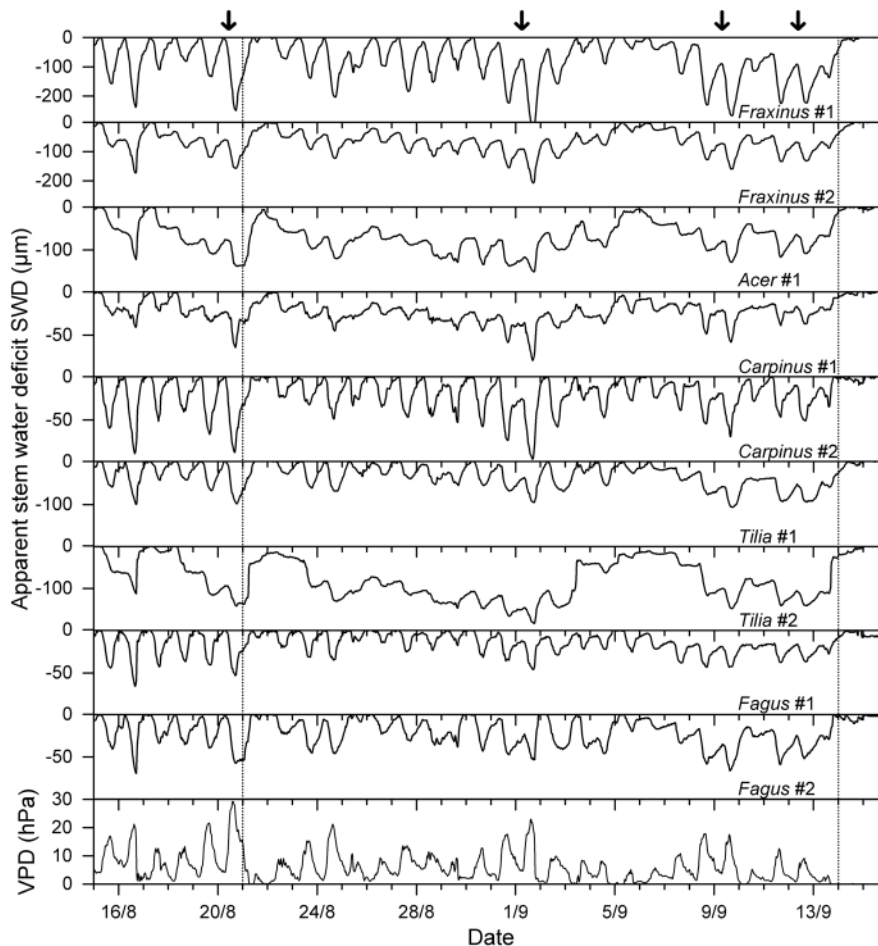


Figure 7. Course of apparent SWD (in μm ; i.e., the deviation of actual radius from the respective stem radius at full hydration) in the nine studied trees from 15 August to 15 September 2009. Arrows show days where the daily SWD_{min} reached high values in several trees. The vertical lines enclose a period with increasing SWD in several trees and a subsequent partial recovery of SWD around the 6 of September. The bottom panel shows the course of the VPD (half-hourly values). Note different scales of the y-axes.

withdrawal decreased proportionally with increasing mean VPD in the 24-day analysis (21 August–13 September) due to higher sap flow rates at the stem base than the stem top when VPD was high (see $J_{\text{rd stembase 24-day}}/J_{\text{rd stemtop 24-day}}$ ratio, Figure 9); in the other four trees, either no relationship existed or appropriate data were not available.

Discussion

Water storage in temperate broad-leaved trees

Apart from succulent plants, trees have the potential to store more water than most other plants, because they are tall at maturity and their leaf area ratio (leaf area per total biomass) is so small (Tyree and Yang 1990). However, for temperate broad-leaved trees, not much is known about the relevance of internal water storage (Scholz et al. 2011). Plants can extract internally stored water from three sources, the elastic shrinkage of vascular tissues, capillary storage at the gas–water interface in xylem conduits and the release via embolism resulting in the dynamic withdrawal of water from conduits during the day (Tyree and

Yang 1990, Sperry and Pockman 1993). Trees can benefit from stored water in purely quantitative terms, i.e., by supplying additional water to the transpiring leaves, but also qualitatively by improving the water status of the canopy in periods of water deficits, thereby increasing carbon assimilation and growth.

Based on synchronous sap flux measurements at the stem top and base, we estimated for the nine trees from five species that 5–22% of daily water use was contributed by withdrawal from stem reservoirs. These results are well within the range given in the more extensive literature on tropical broad-leaved and coniferous trees (<10 to over 50% of daily water use; e.g., Waring et al. 1979, Goldstein et al. 1998, Phillips et al. 2003, Meinzer et al. 2004, Čermák et al. 2007). Mature trees, 25–28 m tall, extracted up to 12 kg water from the stem between stem base and stem top as a daily average in a 30-day period that included both moist and moderately dry time spans. *Fagus*, *Acer*, *Tilia* and *Carpinus* trees (but to a lesser degree *Fraxinus* trees) accumulate large quantities of wood not only in the main trunk but also in the larger branches of the canopy which may also store significant amounts of

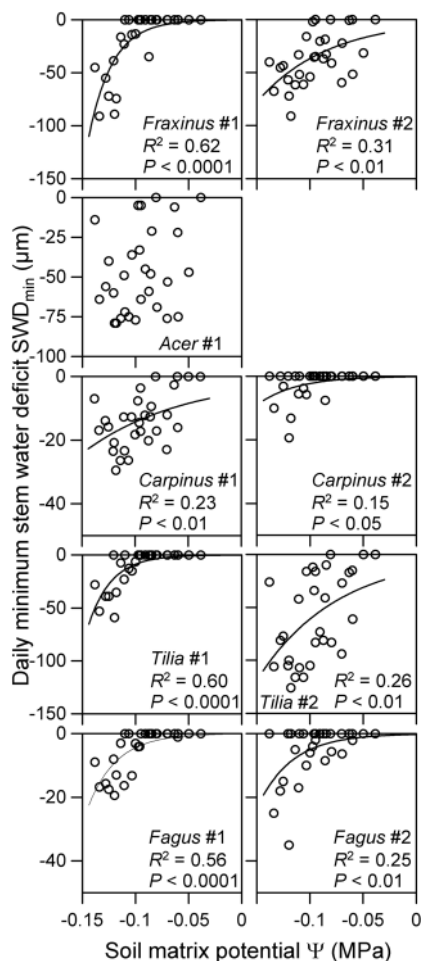


Figure 8. Daily SWD_{min} (μm , morning values) of the study trees as a function of soil matrix potential (Ψ_s , MPa) in 10 cm soil depth. For trees with significant relationships ($P < 0.05$), exponential functions of the type $y = a \times \exp(b \times x)$ are drawn. Note different scales of the y-axes.

water, but were not included in our calculation. The often low canopy base in the first four species (Table 3) indicates that considerable water storage in stem and branch wood was ignored in our study. This may also be true for roots as was found for conifers and tropical trees (e.g., Domec et al. 2006, Scholz et al. 2008). Furthermore, the foliage and perhaps even smaller roots may also act as intermediate water sources that may be capable of reducing the water deficit resulting from daytime transpirative losses (Hao et al. 2008, Scholz et al. 2011). However, in the present study, we focused on the main trunk as it is expected to represent the largest reservoir of stored water contributing to transpiration (Čermák et al. 2007, Betsch et al. 2011) and considered the influence of branches and roots only indirectly through their flux dynamics in comparison with the flow in the stem.

Species differences in the use of stored water

The five species differed by about an order of magnitude in the use of stored water, both with respect to the absolute amount

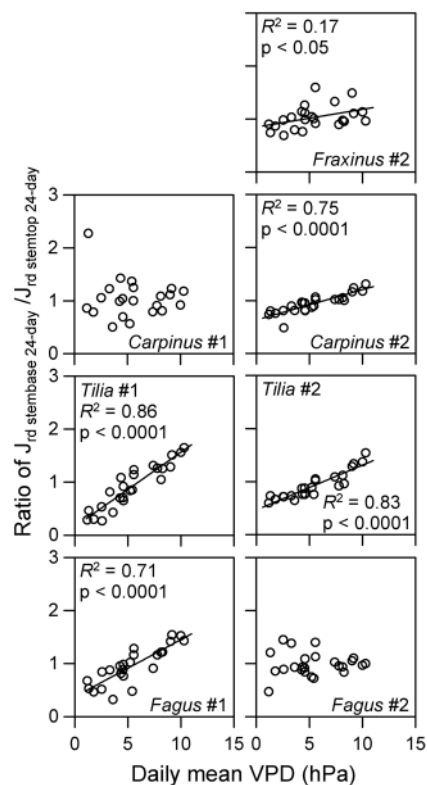


Figure 9. Ratio of the daily sap flow rate at the stem base and stem top ($J_{rd \text{ stembase } 24\text{-day}}/J_{rd \text{ stemtop } 24\text{-day}}$, calculated in the 24-day analysis, see the Materials and methods section) in its relation to mean daily VPD for seven of the nine study trees. Owing to the missing data, *Acer* #1 and *Fraxinus* #1 could not be shown. A ratio >1 indicates a net inflow of water into stem storage and a value below one net outflow. In case of significant relationships ($P < 0.05$), linear regression lines are drawn.

extracted and the withdrawal per stem volume. We found a decreasing use of stored water in the sequence *Tilia* $>$ *Carpinus*, *Acer*, *Fagus* $>$ *Fraxinus*. The *Tilia* trees used large amounts of stored water despite a short trunk length and thus relatively small bole volume and consequently reached high volume-related withdrawal rates. The large stem storage in *Tilia* in comparison with the other three diffuse-porous species may be a result of the about 25% lower wood density of this species (0.43 vs. 0.59–0.67 g cm^{-3}). According to Pratt et al. (2007), hydraulic water capacitance increases with decreasing sapwood density. A similar relationship is confirmed in the present study by a decrease in the use of stored water with increasing wood density when considering only the four diffuse-porous tree species (Figure 6a). *Tilia* with its particularly low canopy base height (ca. 6–7 m) may store much additional water in its extensive branch system, thereby further increasing the availability of stored water in this drought-tolerant species. However, a greater hydraulic capacitance of the sapwood does not only increase the amount of stored water but may also decrease cavitation resistance. Meinzer et al. (2010) discussed a possible trade-off between hydraulic capacitance and cavitation

resistance which would allow tree species with a higher capacitance to have a less safe, but more efficient, conducting system because stored water may help to avoid the development of xylem water potentials that would induce cavitation.

The three diffuse-porous species *Carpinus*, *Acer* and *Fagus* used similar amounts of stored water which matches with comparable wood densities, stem sapwood areas and bole volumes in these trees (except for the *Carpinus* #2 tree with a low canopy base height and smaller bole volume). Betsch et al. (2011) found the relative contribution of stored water to vary between 1 and 50% of daily transpiration in *Fagus* trees with ample water supply. Our estimates of the daily use of stored water in *Fagus* are well below 20%, which probably is caused by the fact that we investigated only the main trunk and not the whole aboveground biomass as Betsch et al. (2011) did. These authors emphasize the importance of stored water in *Fagus* to meet diurnal transpiration requirements and reduce water potential fluctuations which is in accordance with our results. This should similarly be valid for *Acer* and *Carpinus*.

The ring-porous *Fraxinus* trees showed a by far smaller use of stored water in absolute terms which possibly can be attributed to the small sapwood area of this species, since the daily use of stored water has been found to scale with sapwood dimensions (Goldstein et al. 1998). However, this relationship was not significant in the present study and it has to be considered that only two trees per species were investigated. In contrast to the other species, the bole volume in *Fraxinus*, with a great canopy base height, is relatively large. *Fraxinus* trees typically have lower transpiration rates than the other species due to their relatively small canopy leaf area (Hölscher 2004), and thus may require smaller amounts of stored water. The very small amount of stored and withdrawn water per bole volume in *Fraxinus* is in accordance with our low time lag estimate for this species (<4 min between branches and stem base). Among the five studied species, *Fraxinus* can be classified as the most drought-tolerant one with a distinct anisohydric strategy (Carlier et al. 1992, Köcher et al. 2009). *Fraxinus* shows higher values of leaf conductance than most other temperate trees (Besnard and Carlier 1990) and a low sensitivity of sap flow to water shortage (Köcher et al. 2009), while it tolerates large leaf water potential amplitudes without losing vitality (Carlier et al. 1992). Thus, large-sized highly efficient conduits, that supply water to a relatively small leaf area, and a high tolerance of water potential reductions, related to a small water storage capacity, seem to combine in the anisohydric strategy of ring-porous *Fraxinus*.

The temporal coordination of branch, stem and root sap flux

The synchronous flow measurements showed apparent time lags in flow patterns between the branches and stems of a tree in the range of tens of minutes to 1–2 h (except for the

Fraxinus trees and one *Fagus* tree). Such lags are well in the range of values reported for a variety of woody species by Čermák et al. (1982, 1984), Schulze et al. (1985), Loustau et al. (1996), Goldstein et al. (1998), Phillips et al. (1999) and Zweifel and Häsler (2001). According to Čermák et al. (2007) three factors appear to influence the length of the time lag between sap flow at different measuring locations: first, the distance between the selected measuring points, second, the resistance to flow within the conducting elements and third, the dampening effect of the capacitive release of water from storage. A combination of these factors is thought to determine the apparent time lag in most plants (Čermák et al. 2007). In our study, distance seems not to be an important factor for the observed time lags between branches and stem base since it was similar across our trees of comparable size, but the recorded time lags varied greatly between trees and species. This agrees with the statement of Phillips et al. (1999) that the prediction of absolute time lags between flows in trees as a function of tree size may be impractical in mixed species forests. Rather, species differences in the hydraulic resistance of roots, stems and branches and in capacitance should be more important in our sample. This is also in accordance with the results of Verbeeck et al. (2007a), who found in Scots pine trees strong relationships between the use of stored water and several tree traits such as DBH, sapwood area and leaf area, but not with tree height.

Apparent time lags between the onset of transpiration in the morning and the beginning of sap flow at the stem base and in belowground organs of a plant have generally been attributed to the capacitive release of water from storage compartments along the flow path (Schulze et al. 1985, Goldstein et al. 1998, Zweifel and Häsler 2001, Perämäki et al. 2001, Steppe and Lemeur 2004). However, there is a recent debate on the significance of absolute time lags in the onset of flows and the consistency of measured lags with the cohesion theory of water transport in plants (Burgess and Dawson 2008, Phillips et al. 2009). If the plant is seen as a continuum with all parts being hydraulically connected to each other, any depletion of a capacitor along the flow path will immediately cause a slipstream of water from the soil or another source of water within the plant. Thus, the commencement of flows at different points in the plant may be effectively simultaneous but hydraulic capacitance acts to dampen the rate of the response flow. Consequently, Phillips et al. (2009) argued that a lagged response revealed in cross-correlation analysis does not necessarily mean that there was a time lag in the initial response between different positions. Nevertheless, the capacitive release of stored water will lead the stem base sap flow to peak later during the day and consequently there is a lag when the time series are considered as a whole.

The calculated apparent time lags according to measurement at four positions along the root-to-leaf flow path are only

partly consistent as we found an increasing sap flow phase shift with increasing path length from the tree top to the stem base, but interestingly, the sap flow in branches and roots was nearly in phase in almost all trees pointing to the instantaneous transfer of the transpiration signal along the flow path to the roots. On the other hand, stem sap flow frequently appeared to lag considerably behind root sap flow (Table 2). These apparent inconsistencies might have several reasons.

The first explanation is related to the calculation of zero flow. Burgess and Dawson (2008) concluded that absolute time lags between flows in different organs have most often been registered when thermal dissipation sensors were used. In our and most other studies, zero flow was not derived from cutting the xylem and thus it could be erroneous. Given the small absolute flow during the onset of daily transpiration, related measuring errors may have led to misinterpretations.

Second, we used two different types of sap flow sensors in the stem and in branches and roots. We are aware of the limitations inherent to each type of sap flow sensor. One may argue that the response time of the two systems could be different (Burgess and Dawson 2008) and contrasting parts of the sap flow are measured in the stem (only the outermost 2 cm) and in branches and roots (total flow in whole sapwood cross-section). It is further possible that the flow in the outermost one or two tree rings of the stem is responding more rapidly to VPD changes than can be recorded by the Granier sensor which averages over all tree rings in the outermost 2 cm of the sapwood. Point measurements of sap flow with, for example, heat pulse probes would be more appropriate to detect a direct response in sap flux density within one or two annual rings (Gebauer et al. 2008). However, the root flow showed only a minimal time lag to the branch flow (<2 min) and because both were measured with miniature gauge systems, one must conclude that xylem tension signals indeed seem to travel very fast from the leaf to the root in these trees as it was also reported in tall redwood trees by Burgess and Dawson (2008). Furthermore, the length of the negative time lag between stem flow and root flow varied greatly among the trees and species and was zero in *Fraxinus*, which indicates that the specific hydraulics, and not systematic measuring errors, must be the main cause of the finding that root flow typically was 20 to >100 min ahead of stem flow. We therefore assume that root- and branch-sap flow measurements conducted with miniature sap flow gauges and stem sap flow monitored with Granier-type sensors are not the main reason for the time lag patterns found in our trees.

Third, distal branches, the stem and small-diameter roots differ fundamentally in the distribution of conductivity within the respective organ which may influence capacitance and apparent time lags of flow. Upper canopy branches and shallow roots are the two parts of the tree hydraulic system that probably respond markedly to early morning transpiration, while the

stem is likely to show an integrated response diluted by the flow in roots and branches in other parts of the canopy or the soil and dampened by the relatively large stem capacitance. Important elements of this complex hydraulic system were incorporated in the flow and storage model for trees developed by Steppe et al. (2006) on the basis of an electrical analogue or a hydraulic system approach. As an alternative, Chuang et al. (2006) attempted to describe the hydraulic system of trees with a porous media model. Both approaches may produce different results with respect to apparent lags in flow along the flow path.

Relationships between daily SRS and stem water storage

All studied trees showed marked diurnal stem radius fluctuations with a continuous radius decrease from a morning maximum (between 0600 and 0900 h) to a daily minimum normally occurring in the late afternoon or evening (between 1500 and 2000 h). Subsequently, the stem expanded again to reach another morning maximum. These diel changes mainly reflect variations in the water status of the stem (Daudet et al. 2005) but may in part also be attributed to stem radial growth that primarily occurs during night (Köcher et al. 2012b). A contrasting pattern was visible on several rainless days of our measurement period, when VPD was high and soil water supply progressively decreased. On these days, the recharge of stem storage reservoirs during the night was incomplete and the stem radius remained below the previous morning maximum.

How much water is withdrawn from the stores during the day is mainly determined by VPD through its effect on transpiration (Verbeeck et al. 2007b). Consequently, daily SRS was largest on days with high VPD. The refilling of the water stores was primarily a function of soil water availability. We observed a significant effect of a decrease in soil matrix potential (Ψ_s) on the extent of the daily stem water deficit (SWD_{\min}) in four of the five species (Figure 8). The ability of the trees to refill water stores decreased rapidly below a Ψ_s threshold value of -0.1 MPa, indicated by rapidly increasing (more negative) SWD_{\min} values. Exactly the same Ψ_s level was detected by Köcher et al. (2009) as a threshold for leaf water potential and sap flux density to decline in these five species in the Hainich forest. This is evidence in support of the physiological relevance of internal water storage in these trees.

For examining the immediate causes in terms of fluxes of the apparently incomplete recharge of the stem storage as reflected in growing (more negative) SWD_{\min} values, we calculated in the 24-day analysis (see Materials and methods) a rescaled stem base ($J_{\text{rd stembase } 24\text{-day}}$) and stem top ($J_{\text{rd stemtop } 24\text{-day}}$) sap flow. We expected for days with high VPD and large SWD_{\min} a net withdrawal of water from the stem storage and a net recharge when VPD and SWD_{\min} were low or decreased from one day to another. However, no such relationship could be detected; in contrast, the $J_{\text{rd stembase } 24\text{-day}}/J_{\text{rd stemtop } 24\text{-day}}$ ratio rose with

increasing mean daily VPD in some of the trees or showed no relation to saturation deficit (Figure 9). This finding matches with the model results of Verbeeck et al. (2007b), which show a more complete recharge of internal storage reservoirs in Scots pine on days with high VPD than low VPD. The increase in the $J_{rd\ stembase\ 24\text{-day}}/J_{rd\ stemtop\ 24\text{-day}}$ ratio upon an increase in VPD is most probably caused by stomatal closure in response to elevated VPD; four of the five tree species show a sensitive stomatal response to VPD according to the study of Köcher et al. (2009). If leaf conductance is reduced in response to increasing evaporative demand in the first half of the day, transpiration is reduced. Already existing xylem tensions at the tree top may persist and should then result in the maintenance of flux rates at the stem base while sap flux in the canopy already has decreased. This explanation is in accordance with the radius shrinkage data which show largest diurnal radius reductions when VPD is high, indicating a relatively low xylem water potential in the stem, implying a considerable flow of water from the roots to the trunk.

Conclusions

Our results confirm that internal water stores played an important role across the five functionally different temperate broad-leaved tree species. Given the predicted increase in summer drought intensity in many regions of the temperate zone as a result of climate change, it is likely that the functional importance of internal storage in trees will increase in the future. However, considerable species differences in the absolute and relative amounts of stored water used for transpiration seem to exist, which are mainly determined by wood density but most probably also depend on sapwood area (support of hypothesis #1 and 2) and probably also on wood anatomy. The amount of stored water extracted from the stem across the five species was positively correlated with the length of the time lag in flow at stem top and stem base. Ring-porous species may possess a smaller storage capacity in the trunk and thus might lack significant time lags in flow along the flow path. However, the size of the stem store has to be measured in additional ring-porous trees before more general conclusions on the magnitude of this difference between ring- and diffuse-porous species can be drawn. Canopy architecture and the relative size of the volume of main trunk and canopy branches are largely different among temperate tree species; these traits may also influence storage capacity and its distribution in the tree.

The rapid exhaustion of the stem reservoir during periods with reduced soil matrix potential shows that the assumed beneficial role of internal water storage is restricted to periods with ample water supply in the diffuse-porous trees of our study (support of hypothesis #3). In fact, a matrix potential decrease below -0.1 MPa rapidly reduced the stem radius

which indicates that the store was progressively emptied. Moreover, the total daily withdrawal of stored water from the stem did not increase with a VPD increase beyond ca. 3–5 hPa in all species, which implies that the stem reservoir is rapidly exhausted already on days with a moderate evaporative demand. It appears that internal storage plays a much weaker role during the frequent summer drought periods in the sub-continental climate of the Hainich forest. This suggests that internal storage should be an important trait in particular in tree species that grow at mesic to moist sites, while other adaptations must be more decisive in species colonizing xeric habitats. An example is *Fraxinus* with its low absolute storage capacity but efficient morphological, anatomical and physiological adaptations to drought (small leaf area, efficient conducting system and apparent high drought tolerance at the cellular level).

The synchronous sap flux measurements in branches, stem and roots suggest that transpiration-induced pressure signals are often instantly transferred from the leaf to the root level despite the buffering capacity of the internal stores which partly contradicts hypothesis #4. One possible explanation is that the youngest tree rings may represent a direct and highly conductive signal pathway between canopy top branches, stem and roots where the signal can travel rapidly without major interference with older, less conductive conduits that probably play a more important role in storage. We further speculate that this observation may in part be a result of the two different sap flux measuring techniques employed, that register either total or only the outermost flow in the respective xylem segments. Additional studies with synchronous flux measurements in branches, stem and roots, preferably with the same type of sensor, are needed to test if such direct connections along the hydraulic pathway between branches and roots exist.

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Conflict of interest

None declared.

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Appendix

Table A1. Definition, symbols and units of the flux terms used.

Flux	Symbol	Unit
Sap flux density	J_s	$\text{g m}^{-2} \text{s}^{-1}$
Daily sap flux density	J_{sd}	$\text{g cm}^{-2} \text{day}^{-1}$
Daily sap flux density at the stem top	$J_{sd \text{ stemtop}}$	$\text{g cm}^{-2} \text{day}^{-1}$
Daily sap flux density at the stem base	$J_{sd \text{ stembase}}$	$\text{g cm}^{-2} \text{day}^{-1}$
Sap flow rate	J_r	kg h^{-1}
Sap flow rate at the stem top	$J_{r \text{ stemtop}}$	kg h^{-1}
Sap flow rate at the stem base	$J_{r \text{ stembase}}$	kg h^{-1}
Daily water use	J_{rd}	kg day^{-1}
Daily sap flow rate at the stem top (24-day analysis)	$J_{rd \text{ stemtop 24-day}}$	kg day^{-1}
Daily sap flow rate at the stem top (24-day analysis)	$J_{rd \text{ stembase 24-day}}$	kg day^{-1}
Daily use of stored stem water	S_d	kg day^{-1}
Daily use of stored stem water in relation to total daily water use	$S_{d \text{ relative}}$	%
Daily use of stored stem water in relation to bole volume	$S_{d \text{ bole}}$	$\text{kg m}^{-3} \text{day}^{-1}$