Linking xylem diameter variations with sap flow measurements

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Abstract Measurements of variation in the diameter of tree stems provide a rapid response, high resolution tool for detecting changes in water tension inside the xylem. Water movement inside the xylem is caused by changes in the water tension and theoretically, the sap flow rate should be directly proportional to the water tension gradient and, therefore, also linearly linked to the xylem diameter variations. The coefficient of proportionality describes the water conductivity and elasticity of the conducting tissue. Xylem diameter variation measurements could thus provide an alternative approach for estimating sap flow rates, but currently we lack means for calibration. On the other hand, xylem diameter variation measurements could also be used as a tool for studying xylem structure and function. If we knew both the water tension in the xylem and the sap flow rate, xylem conductivity and/or elasticity could be calculated from the slope of their relationship. In this study we measured diurnal xylem diameter variation simultaneously with sap flow rates (Granier-type thermal method) in six deciduous species (*Acer rubrum* L., *Alnus glutinosa* Miller, *Betula lenta* L., *Fagus Sylvatica* L. *Quercus rubra* L., and *Tilia vulgaris* L.) for 7–91 day periods during summers 2003, 2005 and 2006 and analyzed the relationship between these two measurements. We found that in all species xylem diameter variations and sap flow rate were linearly related in daily scale (daily average $R^2=0.61$–0.87) but there was a significant variation in the daily slopes of the linear regressions. The largest variance in the slopes, however, was found between species, which is encouraging for finding a species specific calibration method for measuring sap flow rates using xylem diameter variations. At a daily timescale, xylem diameter variation and sap flow rate were related to each other via a hysteresis loop. The slopes during the

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morning and afternoon did not differ statistically significantly from each other, indicating no overall change in the conductivity. Because of the variance in the daily slopes, we tested three different data averaging methods to obtain calibration coefficients. The performance of the averaging methods depended on the source of variance in the data set and none of them performed best for all species. The best estimates of instantaneous sap flow rates were also given by different averaging methods than the best estimates of total daily water use. Using the linear relationship of sap flow rate and xylem diameter variations we calculated the conductance and specific conductivity of the soil–xylem–atmosphere water pathway. The conductance were of the order of magnitude 10^{-5} kg s^{-1} MPa^{-1} for all species, which compares well with measured water fluxes from broadleaved forests. Interestingly, because of the large sap wood area the conductance of *Betula* was approximately 10 times larger than in other species.

Introduction

The water balance of forest ecosystems is an important factor affecting climate both locally and globally. The major part of water transport in those ecosystems occurs via transpiration. However, water use of trees is not easy to measure accurately. Canopy level measurements give the water fluxes of the area, but partitioning this into transpiration and evaporation remains difficult. Tree and shoot chamber measurements suffer from the adhesive nature of water vapor molecules and sap flow methods are complicated by the xylem structure and water tension (see e.g. Perämäki et al. 2001b).

Diurnal xylem diameter variations measurements are a good indicator of tree water status and use. They have been shown to track closely transpiration rate (e.g. Perämäki et al. 2001a, 2005), leaf water potential (e.g. Ueda and Shibata 2001) and xylem water potential (e.g. Offenthaler et al. 2001) and the daily amplitude is a function of both radiation forcing and soil water availability (Sevanto et al. 2005a). The benefit of diameter variation measurements is that it is a non-destructive and direct tree-level measurement of

water balance. The most accurate and commonly used sensor to measure diurnal xylem diameter variations today is a linear displacement transducer (LVDT) attached to the trunk through a metal frame (see e.g. Neher 1993; Sevanto et al. 2001, 2005b; Daubet et al. 2005) and this set-up requires only few small screws cutting into the xylem, mostly far away from the measurement point. If correctly installed, this system gives almost noiseless data of diameter variation with resolution up to 1 μm (see e.g. Sevanto et al. 2001, 2005a) and even fast changes in transpiration rate can be detected immediately also at the basal diameter of the stem (Perämäki et al. 2005). The water status of the tree is reflected in the overall shrinkage or swelling of the stem. Wet conditions, result in an increase in diameter while during drought the diameter decreases and the daily amplitude of diameter variation increases (e.g. Offenthaler et al. 2001; Sevanto et al. 2005a).

The major shortcoming of this method when estimating sap flow is the difficulty of calibrating xylem diameter variations to represent absolute values of flow rate or water flux. Currently, diurnal xylem diameter variation data can be used to study temporal changes in water fluxes or stem water content of one tree, but comparing water use of two different trees is difficult. Perämäki et al. (2001a, 2005) developed a sophisticated mechanistic model based on the linear relationship between xylem diameter variations and sap flow rates. In principle, this model could be used to calculate transpiration rates from xylem diameter variations. However, it requires accurate measurements of tree size, soil water potential, xylem hydraulic conductivity, and wood elasticity as input parameters and up to date it has only been used in the context of coniferous xylem structure.

In this study we tested whether xylem diameter variation measurements could be calibrated directly with heat-transport based sap flow measurements. Our aims were to evaluate I) whether a simple but general (not tree specific) regression relating xylem diameter variation and sap flow rate could be found, II) what was the largest source of variance between the results of these methods (variance within days, between days, within conspecifics or between species) and III) how large and what kinds of errors would result from estimating sap flow from xylem diameter variation measurements. We also applied the linear theory used by Perämäki et al. (2001a) (see also

Irvine and Grace 1997) to estimate xylem hydraulic conductivity of the soil–xylem–atmosphere pathway and discuss what deviations from linearity in the relationship between xylem diameter variation and sap flow rate mean in terms of sap flow dynamics.

Materials and methods

Species and sites

Sap flow rates and xylem diameter variations were measured on two to three individuals of five deciduous species (*Acer rubrum* L., *Alnus glutinosa* Miller, *Betula lenta* L., *Quercus rubra* L and *Tilia vulgaris* L.) and one individual of *Fagus sylvatica* L (Table 1). The alder trees were type *A. glutinosa forma pyramidalis* 'Sakari'. The measurements were carried out during summers 2003, 2005 and 2006 at the time of full leaves (Jun 1–Aug 30). *Acer*, *Betula* and *Quercus* were studied at Harvard Forest in central Massachusetts USA (42°32′ N 72°10′ W), *Alnus* and *Tilia* in Helsinki, Finland (60°10′ N 24°56′ E) and *Fagus* at Soroe measurement station, Denmark (55° 29′ N 11°38′ E). Individuals of *Acer*, *Betula*, *Fagus* and *Quercus* were mature dominant trees (DBH 8–27 cm, Table 1) in a hardwood forest, while *Alnus* and *Tilia* were juveniles growing in an urban park environment.

The microclimatic data for Harvard Forest was obtained from the nearby meteorological station 300–1,000 m south of the measurement sites. In Denmark the same information was attained from the Soroe micrometeorological station located next to the measurement tree (for detailed information see e.g. Pilegaard et al. 2003) and in Helsinki the photosynthetically active photon flux density (PPFD) and soil water content at 10 and 30 cm depths were measured using Delta-T QS2 type silicon cell PAR quantum sensor and Delta-T ML2x Theta-probes, respectively, in the vicinity of each tree.

The weather conditions at these sites during the measurement periods were comparable. The mean daily PPFD was 411 and 412 µmol m^{-2}s^{-1} at Harvard Forest and Helsinki and 238 µmol m^{-2}s^{-1} in Denmark (note the long measurement period). The percentage of rainy days during the measurement periods was 31% and 23% at Harvard Forest and 36% and 27% in Helsinki and Denmark, respectively. The amount of precipitation at Harvard Forest, 135 and 80 mm for the two measurement periods, was much higher than 4.9 mm in Helsinki. However, the annual precipitation is also much higher at Harvard Forest (2,790 mm) than in Helsinki (700 mm, 30-year average) and the amount

Table 1 Tree characteristics and estimated average slope, elasticity E_r, hydraulic conductance (K_h) and specific conductivity (K_s) of measured tree species

Species	No. of trees	No. of days	DBH (cm)	Sap wood depth (cm)	Sapwood area (m^2)	Daily average slope (kg m^{-3} s^{-1})	E_r (MPa)	$K_h \times 10^{-5}$ (kg s^{-1} MPa^{-1})	K_s (kg m^{-2} s^{-1} MPa^{-1})
Acer rubrum L.	2	7	8.6	3.6	0.0050	−1,360 to −1,515	9,600	2.5–2.7	0.008–0.009
		8	4.3	2.0	0.0012				
Betula lenta L.	3	27	22.8	9.0	0.0384	−260 to −400	8,100	19.0–29.0	0.005–0.008
		32	24.2	7.0	0.0365				
		19	27.4	7.0	0.0409				
Quercus rubra L.	2	7	18.4	1.3	0.0067	−1,820 to −2,175	9,300	3.6–4.4	0.005–0.006
		11	21.2	1.3	0.0078				
Fagus sylvatica L.	1	132	27.0	4.0	0.016	−1,564 to −1,861	9,500	21.0–25.0	0.013–0.016
								16.8–20.0	
Alnus glutinosa Miller	3	27	4.6	2.3	0.0017	−847 to −1,096	8,100	1.1–1.4	0.006–0.007
		33	5.5	2.7	0.0023			0.9–1.2	
		22	5.1	2.5	0.0020				
Tilia vulgaris L.	2	16	4.8	2.4	0.0018	−215 to −307	7,200	0.3–0.4	0.001–0.002
		21	5.4	2.7	0.0023				

The daily slopes were calculated from linear regressions to diurnal xylem diameter variation (m) vs. sap flow rate (kg m^{-2} s^{-1}). The modulus of elasticity is taken for green lumber from a static bending test (Green et al. 1999).

of precipitation in both locations was typical of that time of the year. On the other hand, summer 2003 was exceptionally dry in Europe and there was a clear drought period in Soroe in July, but neither the daily slopes nor the daily degree of explanation of the linear model was a function of radiation forcing (PPFD) or soil water content (data not shown). This indicates that the trees did not suffer from drought (see Sevanto et al. 2005a) and our results are representative of well-watered summer conditions at all sites.

Sap flow measurements

The sap flow rates were measured using Granier-type heat dissipation method (Granier 1985). In this method two thermocouples are mounted on thin needles, one on each. The needles are inserted in the stem above each other about 10 cm apart. The upper sensor is heated with constant power and the sap flow velocity is calculated from the temperature difference between the two needles. The maximum temperature difference occurs when sap flow rate is zero (see Granier 1985).

We measured sap flow rates with two sensors on opposite sides of each stem (primary direction north–south). To minimize the effects of natural temperature gradients, the stems were covered by aluminum foil shades about 30 cm length above and below the sensors. The sap flow rate per sap wood area was calculated as an average of these two and the sapwood area was estimated from core samples taken close to the sensors. The Clearwater-correction (see Clearwater et al. 1999) for needle length exceeding sapwood depth was applied to the data from ring-porous *Quercus*. For *Fagus* we used two sensors at different depths (0–2 and 2–4 cm) and the sap flux (sap flow rate per sapwood area) was calculated from an average of the readings at the two depths distributed evenly through the 4 cm depth. The zero flow temperature difference was estimated from the average of maximum predawn temperature difference of three to five nights in the beginning of the measurement period. The measurements were carried out well below the first living branch. For *Acer*, *Betula* and *Quercus* the measurement height was at about breast height (1.3 m), for *Alnus* and *Tilia* 0.3 m and for *Fagus* 3 m. The measurement interval for *Acer* and *Quercus* was 4 min, for *Betula* 10 min and for *Alnus*, *Fagus* and *Tilia* 30 min.

Xylem diameter variation measurements

Xylem diameter variations were measured about 10–30 cm below the sap flow sensors using LVDTs (Solartron AX/5.0/S; Solartron Inc., West Sussex, UK) attached to a rectangular metal frame mounted around the stem. The frame was attached using metal plates screwed to the stem some 15 cm above the sensors. To eliminate the effects of the living tissue outside the xylem on the diameter variation we inserted two screws through the bark, phloem and cambium so, that they contacted the outer xylem on opposite sides of the stem (see e.g. Sevanto et al. 2005b). The sensor tip rested on one of the screws and the opposite side of the frame on the other enabling us to measure the variation in the distance between the two screws (i.e. the diameter of the stem). Xylem diameter variations were detected one per minute and averaged over 4–30 min periods to adjust to the sap flow sampling rate of the tree. The temperature of each frame was measured using copper–constantan thermocouples and the data was corrected for the thermal expansion of the frame and wood as described by Sevanto et al. 2005b.

Xylem diameter variation is a measure of the pressure field affecting the whole xylem tissue at the measurement level. We tested the homogeneity of the field independently by inserting a second sensor perpendicular to the primary one on three maple, two oak and two birch trees. To estimate the possible effects of wood density on differences seen in the pressure field we took core samples from both the sensor side and the opposite side and measured the dry and fresh density of sap wood (dry weight/fresh volume and fresh weight/fresh volume, respectively). The samples were dried in 60°C in an oven for 48 h.

Analyses

Sap flow in the xylem can theoretically be treated as flow through a porous medium. Knowing the pressure gradient ΔP along the stem, the sap flow rate J through the xylem can be estimated using Darcy's law:

$$J = k\Delta P \tag{1}$$

where k is the conductivity of the tissue.

Changing pressure causes elastic changes in the diameter (Δd), which can be described using Hooke's law:

$$\Delta P = E_r \frac{\Delta d}{d} \qquad (2)$$

where E_r is the elastic modulus of the material in radial direction and d the initial diameter.

Combining Eqs. 1 and 2 results in a linear relation between sap flow rate and diameter variation:

$$J = \text{slope} \times \frac{\Delta d}{d} \qquad (3)$$

where the slope is a product of the axial conductivity k and radial elasticity E_r of the tissue. Evaluation of J using xylem diameter variation measurements thus requires accurate knowledge of these two structural parameters, but on the other hand knowing J and Δd enables us to estimate k and E_r. Typically E_r ranges from a few GPa in softwoods to 10–20 GPa in hardwoods. Unfortunately, there are no measurements of E_r for intact trees and here we used values found in Green et al. (1999) obtained using static bending tests for lumber samples. Xylem k is proportional to the xylem conduit diameter, which varies between species, but also depends on the tree age and habitat. There can be almost two orders of magnitude difference in conduit conductivity (units $m^2 \, Pa^{-1} \, s^{-1}$) of large and small vessels (Sperry et al. 2006).

We calculated linear regressions between xylem diameter variations and sap flow rates using the least-squares method and estimated the hydraulic conductance [$kg \, s^{-1} \, MPa^{-1}$] and specific conductivity (conductance per sap wood area) for each tree using Eq. 3. The statistical significance of the slopes and any differences in the slopes within a day, between days, within conspecifics or between species was tested using Fischer's z test. Because of the within day and between day variation in the relationship between xylem diameter variation and sap flow rate, we tested the accuracy of three different methods of averaging the data. First we calculated the linear regression for all the data points measured on one tree (excluding days of continuous rain fall with no diameter shrinkage, 13 days total), second we calculated the regression for the average daily relationship of xylem diameter variation and sap flow rate (average value at each moment of the day) and third the average of the coefficients of daily regressions. When calculating the daily regressions the xylem diameter was adjusted to zero at each midnight.

We also calculated a modeled sap flow rate using xylem diameter variation data and the obtained hydraulic conductance (Eq. 3, Table 1) and compared that with the measured sap flow rate. To estimate the performance of this model in approximating daily water use we integrated both the measured and modeled sap flow rates over the whole day to give the total amount of water that flowed past the measurement point in 1 day.

Daily amplitudes of diameter variation were calculated by fitting a four-component discrete Fourier series presentation to daily data. The coefficients for each term were determined from Fourier transformation using FFT (Fast Fourier Transformation; Matlab 6.0) algorithm and adjusted by minimizing the deviation of the fit from the data. The fifth and higher terms of the series presentation contributed less than 5% to the power spectrum and could thus be omitted. The amplitude was defined as the difference between highest value of the fitted curve before noon and the lowest value after 9 A.M. This procedure reduced the scatter in amplitudes resulting from either sensor noise or fast daytime variations in microclimate by 15–20% compared to using means of time windows.

Daily time-lags between xylem diameter variation and sap flow rate were determined by correlation analysis where one data set was moved in time with respect to the other to find the highest correlation (see Sevanto et al. 2002; 2003).

Results

Linear regression

Xylem diameter variation and sap flow rate followed a similar diurnal pattern in all species with xylem diameter being smallest when sap flow rate was highest (Figs. 1 and 2). In *Alnus* and *Tilia* the evening recovery of xylem diameter started later than in the other species but that was also reflected in the sap flow rates. The late beginning of recovery was due to the late sunset in Finland (60th latitude) at that time of the year.

Sap flow rate seemed to be linearly correlated with xylem diameter variations in all trees but a linear
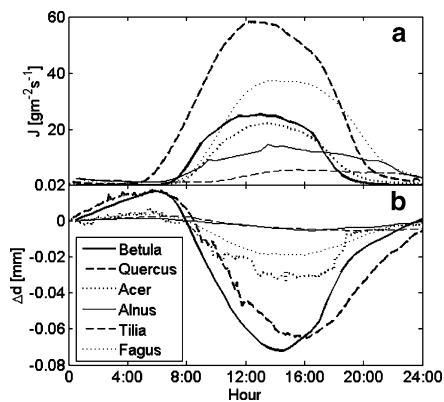
Fig. 1 Daily average pattern of sap flow rate (**a**) and xylem diameter variation (**b**) during the measurement periods. *Betula* was measured in June and July 2005 and *Acer* and *Quercus* in July and August 2006 at Harvard Forest, MA, USA. *Fagus* measurements were made in June–August 2003 at Soroe, Denmark and *Alnus* and *Tilia* in June–July 2006 in Helsinki, Finland. The length of the measurement period varied from 7 to 132 days (see Table 1). The diameter variation data was adjusted to begin at zero each morning

model could explain only 30–74% of the variation (R^2=0.30–0.74) when fitted to all data points (Fig. 3). The poorest degree of explanation was obtained for *Betula* where the daily level of recovery varied most. However, when fitted to daily data the linear model explained more of the variation than when using all the data points. In that case the average R^2 (±SD) of all days was 0.61±0.02 for *Betula*, 0.82±0.01 for *Quercus*, 0.83±0.01 for *Acer*, 0.874±0.004 for *Fagus*, 0.70±0.02 for *Alnus* and 0.62±0.01 for *Tilia*. Sap flow rate and xylem diameter variation could thus be said to be linearly correlated on daily basis and the data sets in Fig. 3 consist of a set of linear daily correlations that vary slightly from each other.

Variation between days and conspecifics

The daily slopes of one tree varied most in *Acer*, *Fagus* and *Alnus* (Fig. 4). For those trees the standard deviation of the daily slopes was >50% of the mean value. For all the other trees it was <40%. The magnitude of the daily slope was not a function of the soil water content, solar radiation, maximum sap flow rate, daily total water use or the daily amplitude of the xylem diameter variation. The variation in the slopes between days could thus not be explained by environmental conditions, the magnitude of sap flow rate or daily water use or the xylem tension in any of the trees (data not shown).

For species that were represented in this study by more than one tree, the average daily slopes (Eq. 2), slopes of daily average relationship or slopes of regressions fitted to all data points did not differ statistically significantly between individuals within one species (Fischer's z test; data not shown) except for birch, where one tree (#3 in Figs. 3a and 4) had a slightly lower slope. The top of that tree was girdled by a woodpecker and the injuries may have resulted in xylem dysfunction and high tension (large diameter shrinkage) was required even for low sap flow rates. For that reason we excluded this tree from the analysis. For *Fagus* we had data from only one tree but measurements over the whole summer period. The slope in June was not statistically significantly different from that in August indicating that neither the phenological state nor the changing environmental conditions affected the water transport of the tree significantly.

Variation between species

The largest variation in the slopes calculated with any of the averaging methods was found between species and the differences in the slopes were statistically significant (Fischer's z test, $p<0.01$) (Table 2 and Fig. 4). Only the slopes of *Betula* and *Tilia* were so close to each other that the difference was not significant. For all species, the slope of regression was lowest if all data points were used, but despite that, within each species the differences between slopes calculated using different averaging methods were not statistically significant.
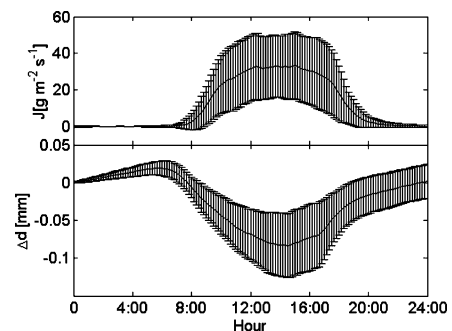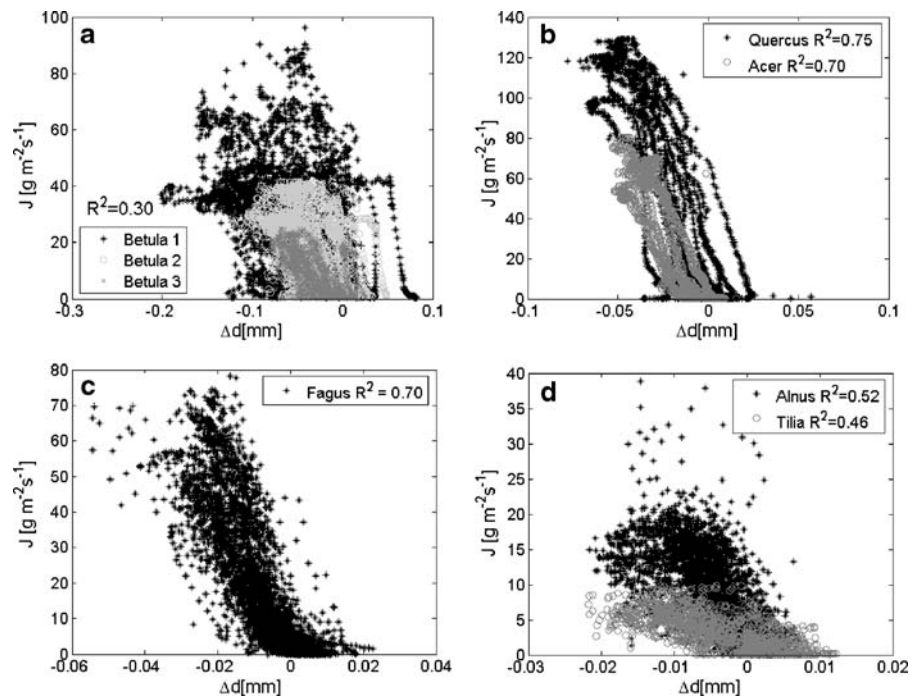

Fig. 2 A typical example of the variation in daily sap flow rate (*top*) and xylem diameter variation (*bottom*). The data is for *Betula* (tree #2) for the whole 32-day measurement period in June and July 2005

Fig. 3 Correlations between sap flow rate and xylem diameter variation for *Betula* (**a**) *Acer* and *Quercus* (**b**) *Fagus* (**c**) and *Alder* and *Tilia* (**d**). In all the other species except *Betula* the regression coefficients of J vs. Δd between individuals did not differ statistically significantly (Fischer's z test). In *Betula* the top of tree #3 was girdled by a woodpecker and the regression coefficients was different from that of trees #1 and #2. The R^2 was the same for all trees also in *Betula*

Variation within a day

In all trees, a typical daily relationship between xylem diameter variation and sap flow rate showed some degree of hysteresis (Fig. 5). For *Betula* and *Quercus* hysteresis was present in 53% and 66% of days, respectively. For all the other species the portion was >70%. However, the morning (0000–1400 hours) and afternoon (1400–2400 hours) slopes did not differ statistically significantly from each other or the daily slope in any case (Fisher's z test) and the hysteresis seemed to result from the stem drying during high transpiration (i.e. almost constant high sap flow rate results in diameter shrinkage), not from diameter changing with different rate compared to increasing or decreasing sap flow rate. The latter would have indicated significant within day changes in the conductivity of the water pathway or in the elasticity of xylem tissue.

The hysteresis could be reduced by applying a time-lag between the xylem diameter variation and sap flow rate measurements. The time-lag giving the best correlation varied from day to day, but in every case sap flow rate lagged behind xylem diameter variations. On average (±SD) the lag was 50 (±30) min for *Betula*, 28 (±16) min for *Acer*, 32 (±9) min for *Quercus*, 45 (±30) min for *Alnus*, 15 (±15) min for

Tilia and 8 (±4) min for *Fagus*. The time-lags did not correlate with the daily maximum sap flow rate, the nighttime level of recovery or the daily amplitude of xylem diameter variation, which indicates that they were independent of the sap flow rate and xylem tension both during the day and night. Correcting for the time-lags did, of course, improve the average
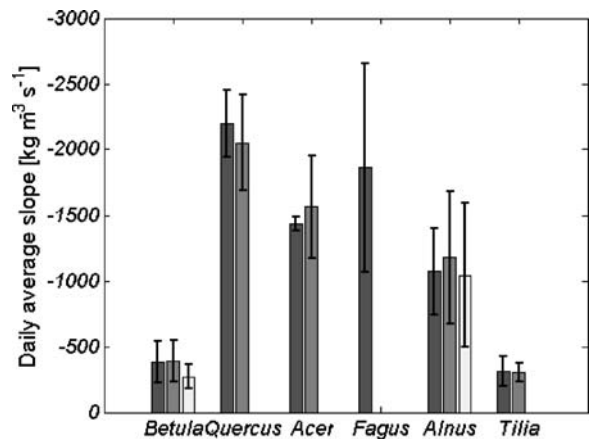

Fig. 4 Daily average slopes of the linear regression between xylem diameter variation and sap flow rate measurements for each tree measured in this study. The individuals of the same species are grouped so that the darkest bar represents tree #1, the second darkest tree #2 and the lightest tree #3. The length of the measurement periods for each tree can be found in Table 1. The *error bars* show the standard deviation around the mean

Table 2 The slopes of linear regression of diurnal xylem diameter variation (m) and sap flow rate (kg m^{-2} s^{-1}) calculated using three different methods of data averaging

Species	Average slope of all data points (±SE) (kg m^{-3} s^{-1})	% Error of daily water use estimate	Slope of daily average pattern (±SE) (kg m^{-3} s^{-1})	% Error of daily water use estimate	Average of daily slopes (±SE) (kg m^{-3} s^{-1})	% Error of daily water use estimate
Betula lenta L.	−260 (±80)	−1.3	−387 (±78)	−1.2	−400 (±52)	25
Quercus rubra L.	−1,820 (±272)	−0.1	−2,175 (±319)	−0.08	−2,100 (±212)	0.5
Acer rubrum L.	−1,360 (±161)	−0.04	−1,515 (±174)	−0.01	−1,510 (±153)	3.2
Fagus sylvatica L.	−1,564 (±60)	−8.3	−1,756 (±15)	0.41	−1,861 (±793)	8.3
Alnus glutinosa Miller	−847 (±125)	−0.2	−970 (±100)	−1.5	−1,096 (±190)	9.7
Tilia vulgaris L.	−215 (±62)	−1.4	−263 (±68)	−7.0	−307 (±63)	9.3

The percentage errors of daily water use are calculated by estimating sap flow rates using diameter variation and the regression.

degree of explanation (average R^2) of the linear model, but it did not affect the average of daily slopes, the slopes of the average daily relationship or the slopes fitted to all data points statistically significantly (data not shown). This suggests that the within day variation was independent of the day-to-day variation in the slopes.

Estimating sap flow rate using xylem diameter variation measurements

To evaluate the power of xylem diameter variation measurements in estimating sap flow we converted xylem diameter variations to sap flow rates using the regressions (see the "Materials and Methods" section) and compared them with measured sap flow rates. Typically, xylem diameter variations overestimated nighttime flow (Fig. 6). On average, the instantaneous sap flow rates was best approximated by using the regression based on the average of daily slopes (*Quercus, Acer* and *Tilia*) or the regression to daily average relationship (*Betula, Fagus* and *Alder*). Daytime behavior depended on the magnitude of the slope so that smallest slopes (Table 2) tended to underestimate sap flow rates whereas the largest overestimated them.

For estimating the daily water use (sap flow rate integrated over the day) the regression to all data points was best for *Betula, Acer* and *Quercus* and the slope of daily average for *Alnus, Fagus* and *Tilia* (Table 2). The average of daily slopes overestimated daily water use by 0.5–25% compared to measured daily water use while the range of error for the two other averaging methods was 0.01–8.3%. The accu-

racy of the daily water use estimate depended on the diurnal residuals and in the case of the regression to all data points the overestimation at night was almost equal to the underestimation during the day, resulting in the overall best performance.

The differences between the regression models using different averaging techniques depended on how the averaging treated the variation in each dataset. For *Betula* the day-to-day variation in the level of recovery in the afternoon was high, resulting in a wide range of diameter variation values with low sap flow rates (Fig. 1), which lowered the slope of the regression fitted to all data points. On the other hand, in *Betula* and *Tilia*, especially, the variation in daily maximum sap flow rates was high (compare with *Acer, Fagus* and *Quercus*) (Table 2), which lowered the magnitude of the slope of the daily average relationship.
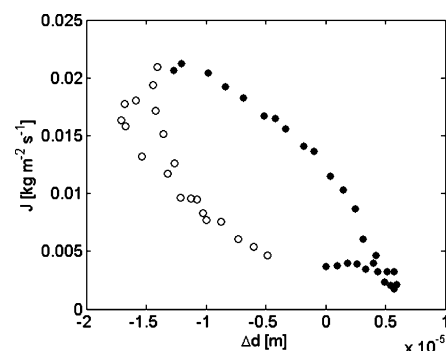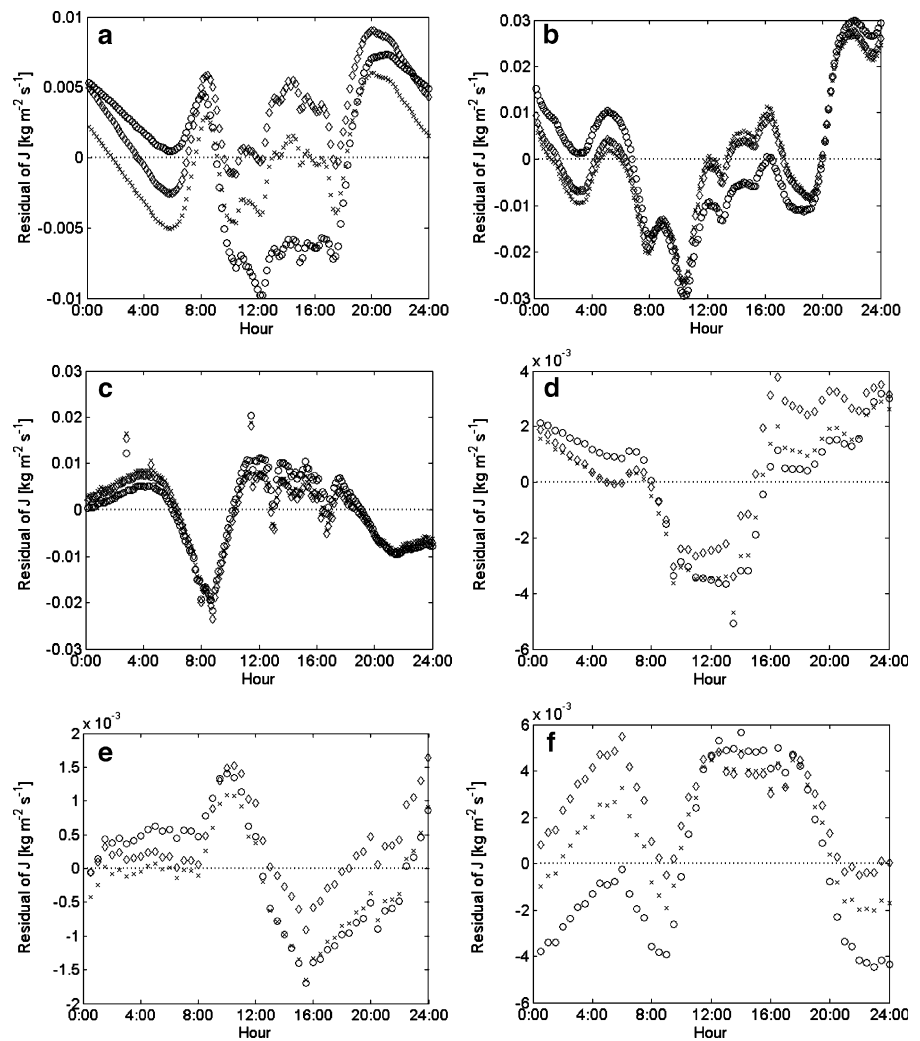

Fig. 5 Typical example of a day with hysteresis in xylem diameter variation vs. sap flow rate (*Alnus*). *Solid symbols* denote morning (0000–1400 hours) and *open symbols* denote afternoon (1400–2400 hours). Diameter variations were adjusted to start at zero at midnight

Fig. 6 Residuals of the cal-culated average daily sap flow pattern compared to the measured sap flow for *Betula* (**a**), *Quercus* (**b**), *Acer* (**c**), *Alnus* (**d**), *Tilia* (**e**) and *Fagus* (**f**). The calculat-ed sap flow rates were based on xylem diameter variation measurements and obtained using regressions between xylem diameter variation measurements and sap flow rate measurements. The *circles* denote residuals of regression to all data points, *crosses* to daily average pattern, and *diamonds* the average of daily regressions

Conductance estimates

To estimate the xylem water conductivity (see Eq. 3) we approximated the elastic modulus with values measured on green lumber (Green et al. 1999) and calculated the hydraulic conductance [kg s^{-1} MPa^{-1}] and specific conductivity (conductance per sap wood area) for each species (Table 1). Hydraulic conduc-tance was highest in *Betula* because of the large sap wood area of that species. Specific conductivities were almost the same for all species. Only *Tilia* had a slightly lower specific conductivity. Interestingly, the conductivity of ring-porous *Quercus* was not higher than that of the diffuse porous species. We also calculated the xylem tensions from Eq. 2 using the elasticity values in Table 1. The maximum tensions ranged from −1.5 MPa for *Tilia* and *Alnus* to

−19 MPa for *Quercus* suggesting that the real elasticity of fresh wood for *Quercus* must be approximately an order of magnitude lower than that used here (for measured xylem tensions see e.g. Daubet et al. 2005 or Domec et al. 2005). Conse-quently, the conductance would be approximately an order of magnitude higher than reported here.

Measurement direction on the stem did not have any effect on the daily diameter variation (Fig. 7), indicating that the pressure field inside the xylem was homogenous. However, the daily amplitude of per-pendicular measurements on the same stem did differ statistically significantly in both oaks and one of the maple trees ($p < 0.01$) suggesting differences in either conductivity or elasticity or both. Neither sapwood depth, nor the sap wood density could explain the differences (data not shown), but in every case the
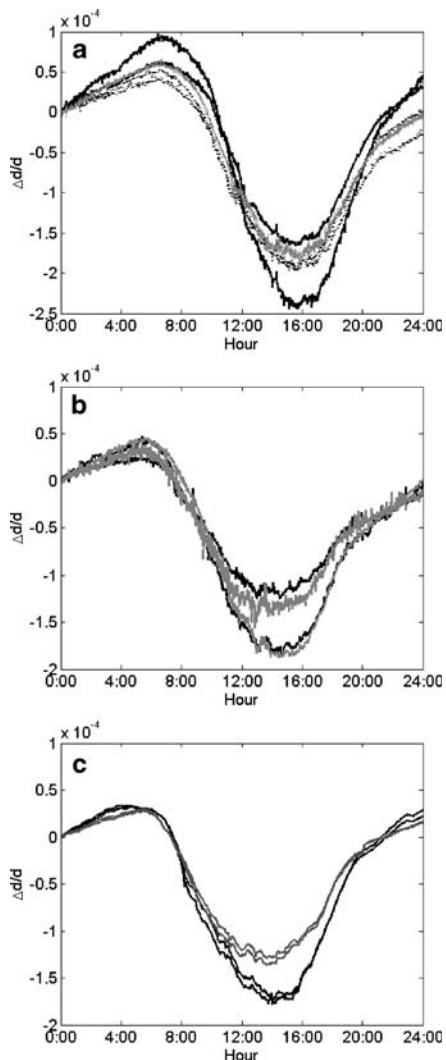
Fig. 7 Daily average xylem diameter variation per the xylem diameter of the stem measured at perpendicular directions on three *Acer* (**a**), two *Quercus* (**a**) and two *Betula* (**a**) trees. *Thick lines* (two lines per tree) mark the first tree, *gray lines* the second and *thin lines* the third (for *Acer*). Diameter variation was adjusted to zero at midnight each day

hydrological cycle and plant physiology and function. In this study, we compared the most widely used heat-transport-based sap flow method (Granier method) with diurnal xylem diameter variation measurements and tested different approaches to calibrate them. The objectives of this study were to test whether a more general than individual-based calibration could be obtained, to determine the largest sources of variation in the relationship between xylem diameter variation and sap flow rate measurements and what kinds of errors would result from estimating sap flow rates using xylem diameter variation measurements.

We based the calibration on linear regressions using the theory developed by Irvine and Grace (1997) and Perämäki et al. (2001a, 2005). The benefit of this approach is that the model parameters are measurable physical properties of the wood material (water conductivity and tissue elasticity) and deviations from the linear relationship can be interpreted as changes in these values. On the other hand, if we knew sap flow rate and xylem tension accurately, this approach could be used for estimating these parameters for different species or trees. Both the within-day (slightly convex shrinkage and concave recovery in Fig. 5) and day-to-day (level of recovery Fig. 3) variation in the relationship between sap flow rate and xylem diameter variation suggest that the most accurate calibration function would be obtained by using a non-linear or generalized linear model. In the first case, the parameters would be purely empirical. In the second they could be interpreted as here and the correction function would then account for the within-day or day-to-day variation in the conductance or elasticity of the tissue.

For finding a calibration function that would not be different for each individual tree, it was encouraging that the average slopes of the regressions did not differ statistically significantly between conspecifics, but did differ between species. This supports the idea that species specific xylem structure is the major source of differences in the relationship between sap flow rates and xylem diameter variation. However, in this study we did not measure on the same species at different habitats and the habitat effect on xylem structure and function remains still to be studied.

The day-to-day variance in the slopes was almost as large as the between species variance in some species (especially *Fagus*; Fig. 4). The reason for this

lower amplitude was found in the direction of the largest branches and the trees with statistically significant differences had a less symmetrical crown than those that did not show any difference.

Discussion

Field measurements of water use in tree-level are important for understanding both the ecosystem scale

remains unclear, because we could not find any environmental factor or structural change causing it. Sevanto et al. (2005a) found that the amplitude of xylem diameter variations was best correlated with photosynthetically active radiation and soil water content, but here we did not find any correlation between those and the daily slope. We did not observe any overall shrinkage in the diameter, indicating drought stress and possible reduction in xylem conductance either. More accurate soil water uptake measurements could possibly shed light to the source of this day-to-day variation. Day-to-day changes in soil–root conductivity could explain changes in tension even if the daily sap flow rates were similar between days.

The conductance values estimated from the regressions were well within the range found in the literature for root, xylem and shoot conductance (see e.g. Zwieniecki and Holbrook 1998; Nardini and Tyree 1999; Bogeat-Triboult et al. 2002; Woodrum et al. 2003; Tisser et al. 2004; Aasamaa and Soeber 2005; Wang 2005). Variation in literature values was approximately plus/minus two orders of magnitude, however, and most measurements were made on small branches or saplings. This emphasizes the difficulty in making such measurements accurately and indicates a need for more reliable methods to measure xylem conductivity.

In this study we used a one point approach for estimating the conductance (i.e. sap flow rate and xylem diameter variation was measured only on one point along the stem) and the values here represent the conductance of the whole soil–xylem–atmosphere-continuum. Therefore, our conductances are in the lower end of the range found for xylem conductance in the literature. In order to measure true xylem conductance more accurately one should measure xylem diameter variations at two heights some distance apart and set the sap flow measurement in between the xylem diameter variation measurements. By taking the difference in pressure changes at these heights (Eq. 2) the conductance of this part of the xylem could be calculated using (Eq. 3). Interestingly, our study suggests that the specific operating conductivity for the soil–xylem–atmosphere-continuum for all the trees was almost the same. This suggests that, despite structural differences, competing species of the same habitat can achieve the same level of resource use.

In this study there are three major sources of error in the calculated conductance values in Table 1. The first and most obvious is the lack of knowledge of the true elasticity of the tissue. The second is the inaccuracy of sap flow and xylem diameter variation measurements and the third the within-day and day-to-day variation in the regression coefficients. To reduce the first, measurements of elasticity of fresh xylem samples should be made. According to Green et al. (1999) an increase in moisture content from 0% to 12% increases the elastic modulus obtained from the static bending test, but there are no studies showing how the elasticity behaves under radial compression. Our results for *Quercus* suggest that the elastic modulus would be considerably lower than reported by Green et al. However, xylem diameter variation and sap flow measurements on *Quercus* are more difficult than on the other species studied here because of the ring-porous xylem structure. The conducting vessels in *Quercus* are large and located close to the outer surface. Therefore, the sap flow velocity and xylem water tension fields inside the xylem are less homogenous than in diffuse porous or coniferous species, which makes both xylem diameter variation measurements and sap flow measurements more unreliable (see e.g. Braun and Schmid 1999). Also, mechanical damage from the inserted screw (dendrometer measurement) or needle (sap flow measurement) may have a more extensive effect on measurements of sap flow and stem diameter where the large vessels of *Quercus* are disturbed. *Quercus* phloem also seemed to be very fibrous compared to the other species and finding the phloem–xylem interface when installing the sensors was not easy. Taking all this into account we were positively surprised of the quality of the data we obtained from *Quercus*, although some caution with these results is justified.

In this study we did not find any way for averaging the relationship between xylem diameter variations and sap flow rate that would have worked best for all the species. This is due to the second and third sources of error in relating xylem diameter variation and sap flow rate measurements: the inaccuracy of sap flow and xylem diameter variation measurements and the within-day and day-to-day variation in the regression coefficients. Compared to measured sap flow rates, the xylem diameter variation measurements seemed to overestimate flow rates during

nighttime (Fig. 6). This may be a result of zero-flow rate level set for too low temperature difference for the sap flow measurements (see e.g. Granier 1985). From the xylem diameter variation data it can be seen that the xylem tension never reaches a constant value that would indicate no flow during the night and the level of recovery depends largely on the water status of the stem (see also Sevanto et al. 2005a). Using xylem diameter variation measurements to estimate the zero-flow conditions for calculating sap flow rates would thus increase the accuracy of the Granier method.

Theoretically, heat-transport based sap flow methods that use constant heating may also underestimate low flow rates because at slow flow velocity heat dissipation to the surrounding tissue becomes important compared to convection (see e.g. Köstner et al. 1998). Therefore, at low flow rates, heat conduction warms up the tissue surrounding the heated needle and when the sap flow rate increases this heat has to be transported away before the sensors give accurate results. There could thus be an inbuilt systematic time-lag in the on-set of measured sap flow rate in the morning (see also Burgess and Dawson, this issue), which should depend on the nighttime sap flow rate. For Granier sensors, the existence of this systematic lag has not been quantitatively demonstrated to date (see also Burgess and Dawson, this issue). Only Braun and Schmid (1999) report observations of time-lags between sap flow rates measured using the Granier-method and a balance. Their lags were even throughout the day and the origin of them remains unclear. However, such a methodological time-lag could explain the present hysteresis in xylem diameter variations vs. sap flow rate (Fig. 5). The time-lags we observed were not constant or did not correlate with nighttime xylem diameter recovery. This suggests that there either is a lag related to the measurement technique that varies from day to day for a reason that is still unknown, or the lag resulting from the measurements (if present at all) is insignificant compared to e.g. water redistribution in the xylem (see Tyree and Yang 1990; Phillips et al. 2004), which would make the relationship between xylem diameter variations and sap flow rate non-linear. The hysteresis here thus seemed to result either from the time-lag or from the diameter decreasing with almost constant sap flow rate in the middle of the day indicating a change in the water content of the stem (more bound water in the afternoon, but not a significant amount of air filled conduits), which was referred to as tissue water storage e.g. by Tyree and Yang (1990) and Zweifel et al. (2001).

To thoroughly understand the within-day and day-to-day variation in the slopes, we need more careful studies that compare sap flow methods also at very low sap flow rates. One option would be to test the Granier system with non-continuous heating (Do and Rocheteau 2002) or try to reduce the possible heat dissipation by keeping the heating at minimum. If still observed, the day-to-day variation and the within day hysteresis open an interesting way to study changes in tissue conductance. For example Henzler et al. (1999) observed that in early morning (from 4 A.M. to 9 A.M.) the root hydraulic conductivity in *Lotus japonicus* increased and after that decreased linearly. If we assume that the variations in the overall xylem water content are small (well watered conditions as here), so that the elasticity is constant, these changes in root conductivity could have caused the convex and concave relations in Fig. 5. In general, a loss of conductivity anywhere along the soil–atmosphere pathway would decrease the slope (same sap flow rate requires larger tension and thus smaller diameter) and an increase in conductivity would increase the slope (the sign convention as in Figs. 3, 4 and 5). Inserting several xylem diameter variation sensors along the stem would enable us even to track the location of conductivity changes. However, analyzing the convex and concave shapes of the slopes more thoroughly would require measurements with higher frequency than once every 30 min. Here the slope in the morning was not statistically significantly different from the slope in the afternoon, which means that the overall conductivity did not change significantly during the day.

The comparison of diameter variation of different directions on the same tree showed that for healthy individuals of these species the transpiration-induced pressure field inside the stem is fairly homogenous. However, if the tree clearly shows asymmetry in the crown or stem, there might be significant differences in values obtained from measurements to different directions and caution should be taken when estimating water use from only one measurement. On the other hand, these differences may open an interesting possibility to detect sectoriality of water pathway in mature trees (see e.g. Orians et al. 2004; Burgess and Bleby 2006).

Conclusions

In this study we tried calibrating diurnal xylem diameter variation measurements for estimating sap flow rates. We did not measure the same species in different habitats and thus the validity of species calibration coefficients can be evaluated only after a careful study of habitat effects. At present, calibrations should be made for each measurement site and the environmental conditions of the calibration period should represent the measurement period. Drought, in particular, may alter the relationship by affecting k. We also showed that a combination of sap flow rate and xylem diameter variation measurements can be used for estimating properties of the water conducting pathway. We found that xylem diameter variation measurements were linearly correlated with measured sap flow rates in daily scale and the largest sources of variance between the linear regression coefficients were between species and day-to-day variation. The between-species variation could be explained by differences in the xylem structure and material properties, but the source of day-to-day variation could not be unambiguously determined with these measurements. In the future more accurate sap flow measurements and more thorough analysis of water flow dynamics are therefore needed to understand the source of variance and its possible connection with water flow dynamics. All in all, this study shows that using sap flow measurements simultaneously with diameter variation measurements significantly increases the amount of information of water flow dynamics inside the stem compared to what would be obtained by either method alone.

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