

Xylem diameter changes as an indicator of stand-level evapo-transpiration

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Xylem diameters of living trees change diurnally. According to the cohesion-tension theory these changes result from changes in sapwood water content. A model based on the assumptions of that theory was used to predict diameter changes from the water vapour exchange in a boreal Scots pine forest. The total evapo-transpiration was measured with the eddy-covariance technique and the contribution of the understorey with open chambers together with the monitoring of the soil water content by the Time-Domain Reflectometry (TDR) method. Comparisons between measured and calculated xylem diameter changes are presented and discussed. The results reveal that diameter changes follow quite well the water vapour exchange in the cases when there was no rain.

Introduction

The diameters of plant stems change diurnally due to changes in the water balance of stem tissues (Kozlowski 1976). The phloem and cambium can change their sizes as a result of hydration and dehydration whereas the xylem can contract and expand elastically as a result of variations in the tension (potential) of xylem water mediated by adhesion between water molecules and the tracheid walls. Varying tension is caused by diurnally changing transpiration, which, according to the cohesion theory (Böhm 1893; *see*

also Zimmermann 1983), drives the ascent of sap. There are few studies where diurnal changes in diameter of the stem were investigated in relation to ambient factors. Hellkvist *et al.* (1980) found a close correlation between the needle water potential and the stem radius. Lövdahl and Odin (1992) found that stem (including bark) variations were mainly caused by changes in relative air humidity at the stem surface. Irvine and Grace (1997) introduced a new system to measure only xylem variations and from these they were able to deduce water tensions in the xylem with a knowledge of the elastic properties of

wood. Laboratory measurements showed that only sapwood contributed to dimensional changes of the xylem and the results agreed with the cohesion theory.

Beside water tension, which Irvine and Grace (1997) analysed, measurements of small xylem diameter changes may provide means of obtaining information about sap flow and transpiration. Perämäki *et al.* (2000) have introduced a model which predicts xylem diameter changes from measured shoot level transpiration data. The calculated diameter values were in good agreement with those measured for a Scots pine tree and the study demonstrated that xylem diameter could be used as an indirect monitor for tree-scale transpiration. Measuring water flow in trees has turned out to be a delicate task (Smith and Allen 1996, Grime and Sinclair 1999) whereas measuring diameter changes does not require very expensive and complicated equipment. Transpiration rates of individual branches could possibly also be estimated by measuring the swelling or shrinking rate of the branch stem. When attempting to estimate transpiration by stands of trees from measurements of transpiration by individual trees together with a spatial upscaling procedure, the low price of diameter sensors and the ease of their maintenance could be of significant advantage.

There are no reports in the literature of attempts to relate diurnal changes in diameter of the xylem quantitatively to stand-scale transpiration. In the present paper, we compare measured xylem variations with those calculated from stand-scale evapo-transpiration (ET), which was measured by the eddy-covariance technique. We partitioned ET into tree and understorey components with soil chamber measurements. The values of forest floor ET deduced from a chamber-based regression were subtracted from ecosystem ET. The resulting canopy transpiration was used as the input for a model introduced by Perämäki *et al.* (2000) in order to calculate the corresponding diurnal xylem diameter change. We describe briefly the measurement techniques and the model and present the results of data analysis and compare measured and calculated daily diameter variations.

Site description

All the measurements were carried out at the Helsinki University SMEAR II field measurement station (Station for Measuring Forest Ecosystem-Atmosphere Relations) in Hyytiälä, Southern Finland (61°51'N, 24°17'E, 181 m a.s.l.) (see Vesala *et al.* 1998). The station is located in a quite homogenous 37-year-old natural managed Scots pine (*Pinus sylvestris* L.) dominated stand about 200 m in all directions from the measurement site, and to the north for about 1.2 km. Under unstable atmospheric conditions the fetch is adequate in all directions (the upwind distance contributing 80% to the flux in the very unstable case (the Monin-Obukhov length being -10 m) is about 100 m (Rannik, 1998)). The terrain is subject to modest height variations. The height of the dominant trees in the stand is 14 m, its zero plane displacement is about 6 m and roughness length is 0.8 m. The mean diameter at breast height (1.3 m) is 13 cm, and the total (all-sided) needle area index varies from 7 to 9, the maximum being in late August. The wood biomass is 47 t ha⁻¹ and the tree density is 2500 per ha. The dominant stand contains only 1% of species other than Scots pine: downy birch (*Betula pubescens* Ehrh.), grey alder (*Alnus incana* (L.) Moench) and aspen (*Populus tremula* L.). The ground vegetation consists of heather (*Calluna vulgaris* L.), lingonberry (*Vaccinium vitis-idaea* L.) and blueberry (*V. myrtillus* L.). The dominating moss species is *Dicranum undulatum*. The annual mean temperature is 3 °C and precipitation is 700 mm. The parent material of the soil is coarse, silty, glacial till and the soil is a Haplic Podzol.

Measurements

Evapo-transpiration

An eddy covariance system was installed in a 73 m high mast at 23 m, 10 m above the forest canopy, to measure ET. The eddy covariance technique is based on the theory of turbulent diffusion in the atmosphere. According to this,

the flux of a gas can be calculated from the time-averages of instantaneous fluctuations of concentrations and vertical wind velocity (*see e.g.* Kaimal and Finnigan 1994, Aubinet *et al.* 1999). The vertical flux is given by

$$F = \overline{w'c'} \quad (1)$$

where w is the vertical velocity and c the gas concentration. The primes denote instantaneous departures from the mean velocity and the overbar represents a mean over a given period. The measurement set-up included an ultrasonic anemometer (Solent 1012R2, Gill Instruments Ltd., Lymington, UK) and a closed-path infrared gas analyser (LI-COR 6262, Licor Inc., Lincoln, NE). The distance of the anemometer from the mast was 3.5 m and a 7 m long heated Teflon (PTFE) tube (inner diameter of 4 mm) was used to sample air from near the anemometer (tube inlet fixed below the sensing head of the anemometer, about 15 cm from the centre) to the gas analyser. A flow rate of 6.3 dm³ min⁻¹ was used to produce turbulent flow. In addition to a membrane filter (1 µm PTFE) at the gas analyzer inlet there was a sintered brass filter at the inlet of the gas sample line to remove particles larger than 50 µm. Pure, dry nitrogen was used as the reference gas for the gas analyser. The fluctuating components were extracted from the turbulent records by linear detrending (*see e.g.* Rannik and Vesala 1999). After an averaging period of 0.5 h, the delay time for H₂O was obtained by determining the maximum unrotated vertical covariance. Finally, the flux was corrected for the imperfect frequency response of the system (damping of fluctuations in sampling line, frequency response of the gas analyser) according to Moore (1986) by using the model co-spectra of atmospheric surface layer turbulence (Kaimal *et al.* 1972). A more detailed description of the operation of the set-up is given by Rannik (1998). PAR radiation above the canopy was measured with a Li-Cor 190 SB sensor attached to a separate tower at the height of 15 m.

Diameter changes

The xylem diameter variations were measured

once per minute by Sylvac industrial diameter transducers (Sylvac Inc., Switzerland) and by Solartron (Solartron Inc.). A rigid steel frame was fixed around a tree and the transducer was attached to the frame. An area of about 1 cm² of phloem, bark and cambium was removed on opposite sides of the tree. The areas were covered with aluminium plates and small screws were attached through them. The frame was set to rest on the screws. The measurements were corrected for the effect of temperature on the expansion of the steel frame (the coefficient of linear expansion of the steel used for the frame was 10 × 10⁻⁶ K⁻¹). A detailed description of the measurement system is given in Perämäki *et al.* (2000). The Sylvac measurements have been running on a tree of diameter 20 cm at the height of 2.5 m for four years. Similar measurements were also carried out at the same height on three other trees of diameters 8 cm, 10 cm and 15 cm for three weeks in September 1999 (the 10 cm tree was measured by Solartron and the others by Sylvac). All the diameter variations followed the same pattern the only difference being in the amplitude. The amplitude of the variations of the 20-cm tree was found to be close to the average of the others. This may be a result of the larger amount of heartwood, which does not contribute to the diameter changes (Irvine and Grace 1997). We use this tree as the representative when comparing measured xylem variations with those calculated from ecosystem ET.

Soil and ground

The volumetric soil water content was determined with the Time-Domain Reflectometry (TDR) method (Tektronix, TDR 1502, Tektronix Inc., USA). Soil water potentials were calculated from the soil water content with separately determined soil water retention curves. Soil and air temperatures were measured using silicon temperature sensors (Philips KTY81-110) and shielded constantan thermocouples respectively. The water exchange of the understorey vegetation was measured for five days from 28 June to 2 July 1999 with two open chambers, which

have been described in detail by Hari *et al.* (1999). The measurements were done in a transient mode i.e. the transpiration was measured using the concentration increase in the chambers. The measurements were done in 70-s periods during which the lid of the chamber was closed, and a regulated air flow with known H₂O concentration was introduced into the chamber. An equal amount of air was sucked from the chamber to the H₂O analyser. The transpiration was calculated from the mass balance for the incoming and outgoing air.

The model

To deduce stem diameter changes from evapotranspiration measurements we used a modified version of a sectional water flow model developed by Perämäki *et al.* (2000). The model calculates the diameter changes of a tree from measured transpiration and soil water content according to the cohesion-tension theory: axial water flow is caused by a pressure gradient, and water deficit causes water tension which leads to xylem diameter changes. Diameter changes are assumed to be reversible. The model tree is divided into equally long segments and the mass balance equation

$$\frac{dm_{w,i}}{dt} = Q_{in,i} - Q_{out,i} \quad (2)$$

where $m_{w,i}$ is the mass of water (water content) in a segment i and $Q_{in,i}$ and $Q_{out,i}$ are the corresponding values of mass flow rates, is solved for each tree segment. The inflow rate is calculated by Darcy's law, which combines water flow with the pressure gradient of a segment

$$Q_{in,i} = \frac{k}{\eta} \frac{P_{i-1} - P_i}{l} A_i \rho \quad (3)$$

where k (m²) is the water permeability of wood, η is the dynamic viscosity (Ns m⁻²) of water, l and A_i are the length (same for each segment) and area of sapwood of a tree segment respectively, and ρ is the density of water. The changing hydrostatic pressure along the stem is taken into account in the values of the pressure. Hooke's law gives the relationship between changes in

diameter d_i and pressure P_i

$$\frac{dd_i}{dt} = E_r \frac{1}{d_{0,i}} \frac{dd_i}{dt} \quad (4)$$

where E_r is the elastic modulus of wood in the radial direction and $d_{0,i}$ is the initial diameter of the xylem segment and a geometric equation for cylindrical stem segments reveals the relation between changes in diameter and water content of a segment

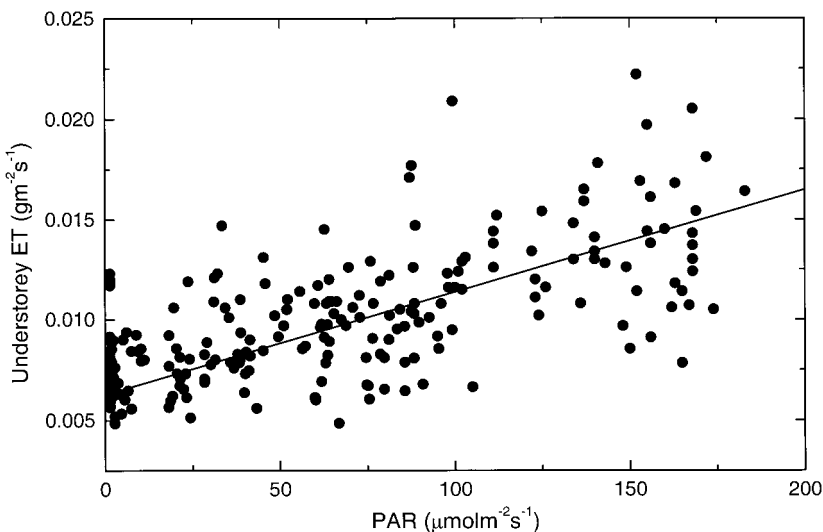
$$\frac{dd_i}{dt} = \frac{2}{\pi \rho l d_{0,i}} \frac{dm_{w,i}}{dt} \quad (5)$$

Substituting Eq. 3 for $Q_{in,i}$ in Eq. 2 and re-

placing $\frac{dm_{w,i}}{dt}$ in the same equation with a result of its calculation with Eq. 5 allows us to rewrite Eq. 2 to express the relationship between the diameter change and the flow rate. This equation is solved with Eq. 4 by applying the fourth-order Runge-Kutta method (Press *et al.* 1989). The pressure difference between successive tree segments is updated after each time step. Transpiration is used as input data for the outflow from the tree, and the inflow of each segment is the outflow of the previous. The other input is soil water tension which is linked to the tension at the base of the tree by Darcy's law using fine root conductivity as the conductivity between the soil and the tree. In other words, transpiration and soil water tension serve as boundary conditions for solving the flow through the tree.

We used the so-called big-leaf approach (e.g. Edwards *et al.* 1986) where the canopy transpiration occurs at the definite height of highest transpiration calculated from the vertical leaf area distribution using the exponential Beer-Lambert law for shading of the foliage. The transpiration rate was calculated from the water vapour flux measured by EC and scaled with LAI and tree density. The contribution of the understorey (based on the soil chamber measurements) was subtracted from the transpiration. The characteristics of the model tree were made to correspond to those of the stand determined by harvesting. The mean values of the diameter and needle area are based on a sample of four trees. The needle area was calculated from the

Fig. 1. The light response of understorey evapo-transpiration with the fitted curve. Radiation was measured above the canopy and reduced with the Beer-Lambert law. Evapo-transpiration was measured with flow-through chambers. The equation of the curve is $y = 0.000051x + 0.0063$, where y is evapo-transpiration in $\text{g m}^{-2} \text{s}^{-1}$ and x is PAR in $\mu\text{mol m}^{-2} \text{s}^{-1}$. $R^2 = 0.48$. The data was collected from 26 June to 2 July 1999.



sapwood area according to Palmroth *et al.* (1997) and it was found to be 50 m^2 .

Results and discussion

We compare the measured and calculated diurnal stem diameter changes for a period of 12 days from 15 to 26 June 1999. The model includes three parameters: the elastic modulus of wood, the conductivity of sapwood, and the fine root conductivity, the values of which must be fitted against the measured diameter changes. The fitting was made using the data of 16 June 1999 (*see Perämäki et al.* 2000).

To get an estimate for water flux coming from understorey, the light response curve was calculated from the data of three days of the soil chamber measurements in 1999. The PAR values are based on the above-canopy measurements corrected with the Beer-Lambert law for absorption of foliage consistently with the approach used in the model. We also determined the response curve using below-canopy PAR measurements (*see Vesala et al.* 1999) but the results were found to be independent of the method. The measured understorey water vapour flux was linearly correlated with the calculated PAR ($r = 0.69$, $p = 0.005$) (Fig. 1). Comparing with the EC measurements of the total evapo-transpiration, the understorey seems to contribute 30% at the maximum.

Measured values for evapo-transpiration rate for the period 15 to 26 June 1999 were used in the analysis (Fig. 2). Using the fitting in Fig. 1, we subtract the understorey contribution from the total ET and use the result as an input in the model. The simulated and measured stem diameter changes were compared with each other (Fig. 2b). The curves are adjusted to begin at zero in the beginning of the period. Comparing Figs. 2a and b shows that diameter changes reflect the pattern of evapo-transpiration. The simulated curve especially resembles the ET curve. The general patterns of the simulated and measured curves are in good agreement and the inter-daily variations are also clearly apparent in the calculated values. The model is also able to predict variations of short duration (*see insert in Fig. 2b*), which are mainly caused by the rapid changes in PAR, although the calculated diameter changes are occasionally much larger at daytime. It should be noted that a significant random error is inherently present in all measured 0.5 h flux values because of the statistical nature of turbulence. For the measurements considered here, the most frequent error is about 10% (Rannik and Vesala 1999). At nights, the modelled curve is typically more flat and reaches the largest value earlier than the measured one. This is mostly due to the underestimation of ET measured by EC under the nocturnal stable atmospheric stratification (these values are included since ET is very small anyway, *see Fig. 2a*).

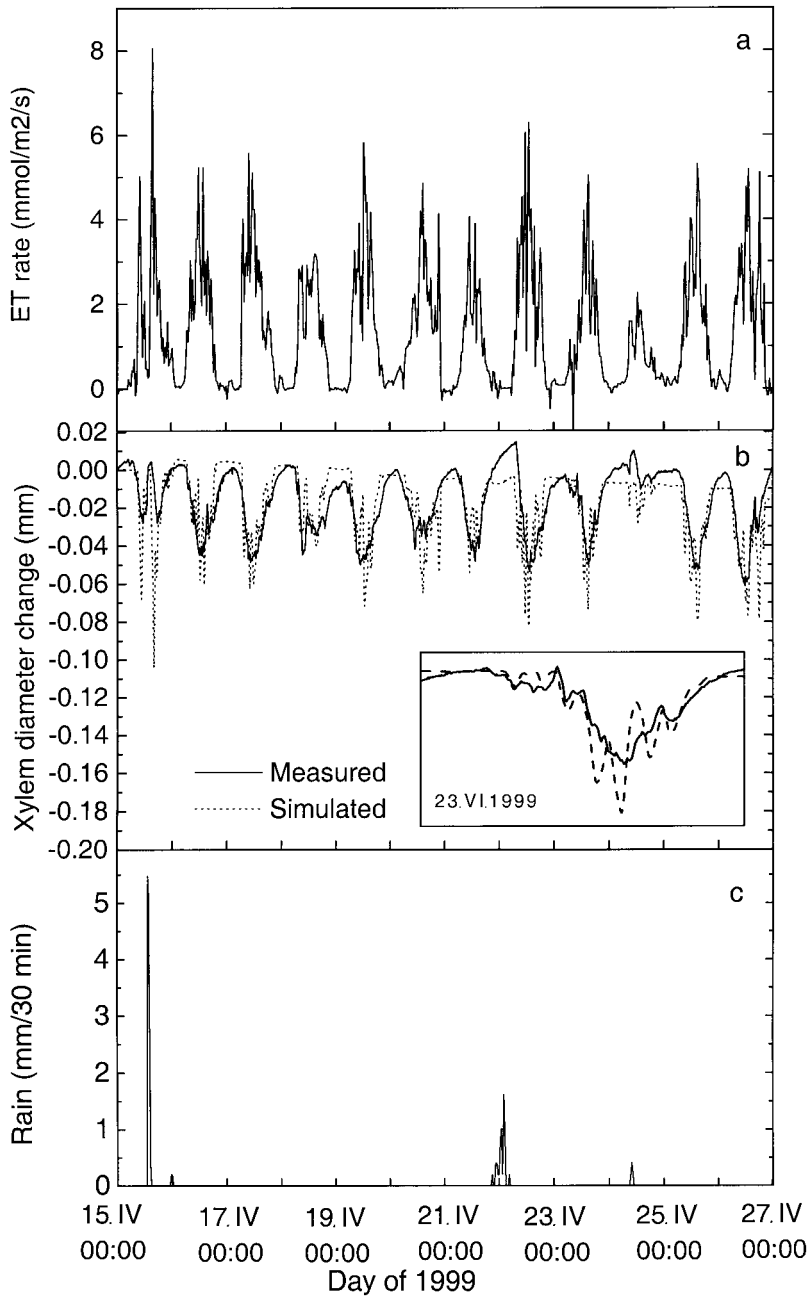


Fig. 2. — **a:** Evapo-transpiration rate for the days from 15 to 26 June 1999. — **b:** Measured (solid line) and model calculated (dot line) xylem diameter changes. The zero level is adjusted to zero at the beginning of the measurement period. — **c:** The rainfall events during the measurement period.

Some of the discrepancy may also result from the inability of the model to predict the swelling of the tree correctly. One reason for this might be the higher root resistance in the afternoons caused by the drying of the soil in the immediate neighbourhood of the roots, which is not taken

into account in the model. The overall decreasing trend in the zero level of the simulated values results from the increasing soil water tension during the period, i.e. a constant soil water tension implies a constant zero level. Since it is observable only in the simulations, the coupling

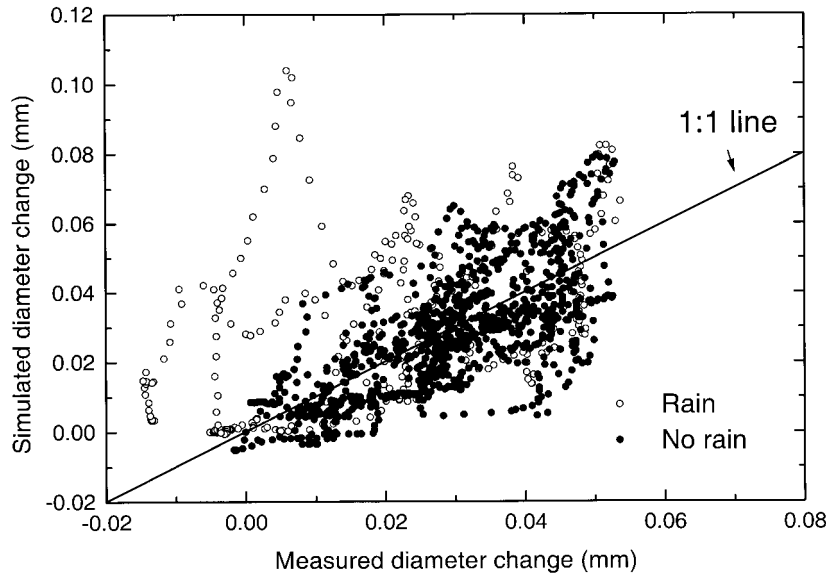


Fig. 3. Measured versus calculated day-time xylem diameter changes. The days with no rainfall (circle) and rainfall more than 1 mm/30 min (open circle) separated. $R^2 = 0.75$ for days with no rain.

between the tree and the soil may be too strong or the discrepancy might reflect deficiencies in the description of the stem fine structure. A few rainfall events occurred during the measurement period (Fig. 2c). The largest simulated diameter changes in day-time are caused by the evaporation during and just after rainfall and the significant swelling of the measured stem diameter in the night between 21 and 22 June is due to rain as well (Fig. 2b and c). The measured diameter changes were plotted against simulated in conditions when there was no rainfall during the day or it had rained more than 1 mm per 30 min (Fig. 3). Night-time values (from 6 pm to 6 am) were not included. The effect of evaporation from wet surfaces during and after rain can be seen in the large deviations. However, the overall compatibility between measured and simulated diameter changes is rather good in the cases when there was no rain.

Conclusions

The earlier study with this model (Perämäki *et al.* 2000) showed that xylem diameter variations follow the measured shoot transpiration and can therefore be said to result from changes in water

balance in the xylem as predicted by the cohesion-tension theory. In this study the model was used to link the evapo-transpiration of the whole ecosystem with tree stem diameter changes. The results revealed that diameter changes follow quite closely the water vapour exchange in the cases when there was no rain.

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