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ORIGINAL ARTICLE

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Wood diameter indicates diurnal and long-term patterns of xylem water potential in Norway spruce

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Abstract The stem diameter of adult Norway spruce trees was measured to see whether changes in xylem water potential lead to detectable radial deformation of the wood. The dendrometers used in these experiments measured only the dimensional changes of the woody cylinder (sap- and heartwood). Wood diameter was measured close to the ground and just below the living crown. After correction for thermal expansion of dendrometers and wood, diurnal variation of wood diameter ranged between 50 and 180 µm. Psychrometric measurements showed that xylem water potential varied in parallel to wood diameter. Diameter changes were always more pronounced at the higher stem position and exhibited a clear diurnal pattern. During the day, wood diameter decreased with increasing vapor pressure deficit and transpiration rate and with decreasing twig water potential. At night, the wood re-expanded but did not always reach the dimension of the previous day. Pre-dawn wood diameter decreased during periods of soil drought, a process which rapidly stopped and reversed after rain events. On several days, oscillation in wood diameter was observed during the mid-day hours. The oscillation had a period of approximately 50 min and showed a phase shift between different stem heights. All observed patterns of wood shrinkage and expansion were consistent with the hypothesis that xylem water tension leads to an elastic contraction of xylem conduits. The results demonstrate that xylem diameter is more suitable than whole-stem diameter for monitoring changes in xylem water potential.

Keywords Dendrometry · Wood diameter · Xylem water potential · *Picea abies*

Introduction

Diurnal fluctuations in the stem diameter of trees have been known for over 100 years (Friedrich 1897a, b) as a side-product of dendrometer studies mainly aimed at monitoring radial growth over prolonged periods. Generally, these observations have been thought to reflect differences in the water status of the stem during the course of the day (Hinckley and Bruckerhoff 1975; Wronski et al. 1985; Brough et al. 1986; Simmoneau et al. 1993). As the usual experimental setup measures changes in whole-stem diameter or circumference, it was mostly unclear which parts of the stem were responsible for the shrinkage and expansion observed. Most authors assumed that they took place primarily or exclusively in the phloem and bark, rather than in the xylem, which is composed mainly of dead conducting elements. However, Friedrich (1897b), Haasis (1934) and Daum (1967) reported diameter changes of the stem wood and Bode (1923) observed in situ tension-induced contractions of single vessels with a horizontal microscope. Brough et al. (1986) reported that the xylem accounts for about one-quarter of the stem diameter changes in *Malus pumila* trees with a diameter of 4 cm. This mechanical deformation of the sapwood is a result of the negative hydraulic pressure in the xylem conduits. Changes in wood diameter generally have received little attention. Linear (Molz and Klepper 1972; Molz et al. 1973) or non-linear (Parlange et al. 1975) diffusion models accounting for the movement of water between phloem and xylem and, therefore, including a time-lag between xylem water potential (ψ^{xylem}) and diameter changes, successfully relate stem diameter to ψ^{xylem}. Parlange et al. (1975) also found a good correlation in *Pinus resinosa* with a lag of 2 h between twig water potential (Ψ^{twig}) and stem diameter. With a novel dendrometric setup measuring only xylem diameter changes, Irvine and Grace (1997) found that xylem diameter, after calibration and without a time-lag, can be used as a substitute for direct measurements of ψ^{xylem}. This is very welcome, because other methods of measuring water potential are either unsuitable for automatic and prolonged measure-

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ments (pressure chamber) or are complicated to install, difficult to maintain and error-prone in the field (stem psychrometers, stem tensiometers).

Changes in xylem diameter offer several advantages over whole-stem diameter for long-term monitoring of tree water status in the field as (1) the relationship with ψ^{xylem} is direct, linear and immediate (Irvine and Grace 1997) and does not require a model of phloem capacitance and the diffusion between phloem and xylem, (2) the cambium at the measurement points is locally destroyed and, therefore, contraction and expansion of the xylem are not obscured by diameter growth, (3) changes in ambient humidity and temperature, which also result in shrinkage and swelling of dead bark tissue (Lövdahl and Odin 1992), do not interfere when the exposed xylem is protected from local water loss. Here we present long-term observations on xylem diameter variation in the field using the approach of Irvine and Grace (1997) and explore their potential for long- and short-term monitoring of tree water status.

Materials and methods

Measurements were made on two 60-year-old Norway spruce (*Picea abies* [L.] Karst) trees growing on experimental plots no. 184 and 185a of the FWF Special Research Program 008 near Kreisbach, Lower Austria (48°05N, 15°39E, 480 m a.s.l.) The site is located on a northward slope with a stagnic cambisol. Tree diameters at breast height were 32.9 and 40.4 cm. Sapwood depth (4–5 cm) was determined with an increment borer.

The dendrometer consisted of a linear displacement transducer (LMT50 S; Gefran, Provaglio d'Iseo, Italy) mounted on a metal frame around the stem as described by Irvine and Grace (1997). A bolt fixed to the frame and the measuring tip of the spring-loaded transducer on the opposite side were the only points in the measurement plane in contact with the stem. Bark and phloem were removed at these two points so that only wood diameter changes (Δd^{xylem}) were measured. The exposed xylem was covered with silicon grease to prevent local water loss. Dendrometers were installed at 1.5 m stem height and just below the living crown at 13.7 and 15 m. The output of the displacement transducers, measured with a resolution of 0.4 µm, was logged every minute and stored as 15-min averages. Readings were corrected for thermal expansion of frame and wood using the linear expansion coefficients of α_{iron} 12 ppm/°C (interpolated from Lax 1967) and α_{wood} –4 ppm/°C (Irvine and Grace 1997). Ambient air temperature was used to calculate thermal expansion, since preliminary experiments had shown that the temperature of the uninsulated metal frame lagged ambient air temperature by less than 5 min (the dense canopy and the shiny metal surfaces prevented heating of the dendrometers by direct sunlight). Calculating thermal wood expansion from ambient temperature introduces a small error, because diurnal temperature amplitudes are smaller in the wood than in the surrounding air. However, separate experiments showed that this temperature difference was never higher than 5°C, resulting in a maximal error of 3% of the observed diameter change. Sap flow was measured with the tissue heat balance method (constant heating power; Čermák et al. 1973), using a P4.1 sap flow meter (EMS, Brno, Czech Republic). Two sensors were installed at opposite sides of the trunk at 2 m height. Sap flow (in kg h^{-1} cm^{-1} xylem circumference) was measured every minute and condensed to 15-min averages. Sap flow per tree (J) was calculated from the mean of both sensors multiplied by the xylem circumference at the measuring height.

Relative humidity and air temperature in the canopy were measured with an RMP45 sensor (Vaisala, Helsinki, Finland). Precipitation (ARG100 tipping bucket rain gauge; Campbell Scientific, Logan, Utah, USA) and shortwave radiation (8101 pyranometer; Schenk, Vienna, Austria) were measured in an open area at about 500 m distance from the forest stand. Data on soil water content from time domain reflectometry (Trase; Soilmoisture Equipment Corp., Santa Barbara, Calif., USA) were kindly provided by H. Schume (Institute of Forest Ecology, University of Agricultural Sciences, Vienna).

Xylem water potential (Ψ^{xylem}) was determined with stem psychrometers (P.W.S. Instruments, Guelph, Ontario, Canada; Dixon and Tyree 1984), controlled and logged with a CR7 datalogger (Campbell Scientific) equipped with a psychrometric module (Wescor, Logan, Utah). To install the psychrometers, a plug of bark, phloem and cambium slightly larger than the diameter of the psychrometer was removed. The xylem surface was gently abraded and thoroughly rinsed with distilled water. Silicon grease was used to produce an airtight seal between psychrometer chamber and xylem surface. After clamping the psychrometer to the stem, the remaining gap between sensor and bark was filled with silicon grease to prevent drying of the exposed xylem. Psychrometric readings were corrected for ambient temperature and temperature gradients between xylem surface and psychrometer chamber. Psychrometric measurements could never be continued for more than 10 h, due to the formation of resin droplets which led to sudden contamination of the thermocouple.

Water potential of 5–10 cm long twigs (Ψ^{twig}) was determined with a pressure chamber (Model 3000; Soilmoisture Equipment Corp.). Each data point is the mean of two or three replicates taken from different branches of the mid-crown.

The temporal pattern of Δd^{xylem}, J, and vapor pressure deficit (D) was examined for time-lags using cross-correlation statistics (SPSS 8.0.0 statistical software package, SPSS Inc., Chicago, Ill., USA). Cross-correlation was calculated for each day separately. Twenty-four hour time series were used to compare Δd^{xylem} at the upper measuring position with J and Δd^{xylem} between the two stem heights. In contrast to J and Δd^{xylem}, D sometimes showed no well-defined peak but remained at a plateau which could continue until the late afternoon hours. Therefore, to identify time-lags between D and Δd^{xylem}, we limited analysis to the periods when D was rising continuously. These were the morning hours from 5:00 until 12:00 noon.

Results

Changes in wood diameter showed a marked diurnal pattern characterized by a continuous shrinkage from the onset of transpiration, with minimal wood diameter in the early afternoon. Subsequently, the xylem expanded again to reach its maximal diameter in the early morning hours. The psychrometric determination of Ψ^{xylem} showed a linear relation between wood diameter and xylem water tension (Fig. 1). Wood diameter, D, J and Ψ^{twig} varied in parallel over the day (Fig. 2). Changes in wood diameter were always more pronounced at higher stem positions (Fig. 3). The amplitude of daily variation ranged between 30 and 80 µm at 1.5 m and between 50 and 120 µm at the upper measurement point (13.7 or 15 m). There was no time-lag between Δd^{xylem} at the upper position and D (Table 1), which suggests that changes in atmospheric vapor pressure deficit resulted in immediate changes in Ψ^{xylem} just below the crown. However, Δd^{xylem} at 1.5 m lagged that at 13.7 m by up to 110 min. During a drought period of 3 weeks, the predawn xylem diameter shrank continuously with decreasing soil water content. The shrinkage ceased when soil water content increased after rainfall and the wood re-expanded rapidly (Fig. 4).

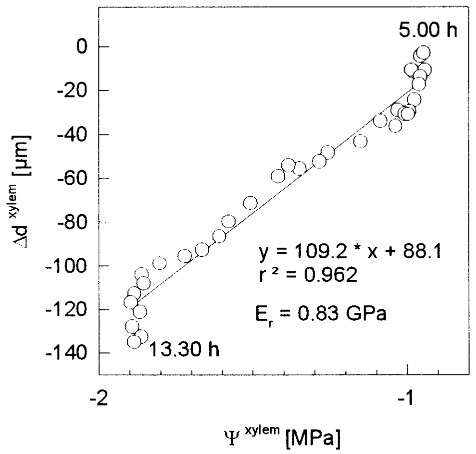

Fig. 1 Relationship between changes in wood diameter (*Δd*^{xylem}) and xylem water potential (*Ψ*^{xylem}) measured with a stem psychrometer at 15 m height on a Norway spruce tree. The elastic modulus (E_r) was calculated from the linear regression as explained in the text

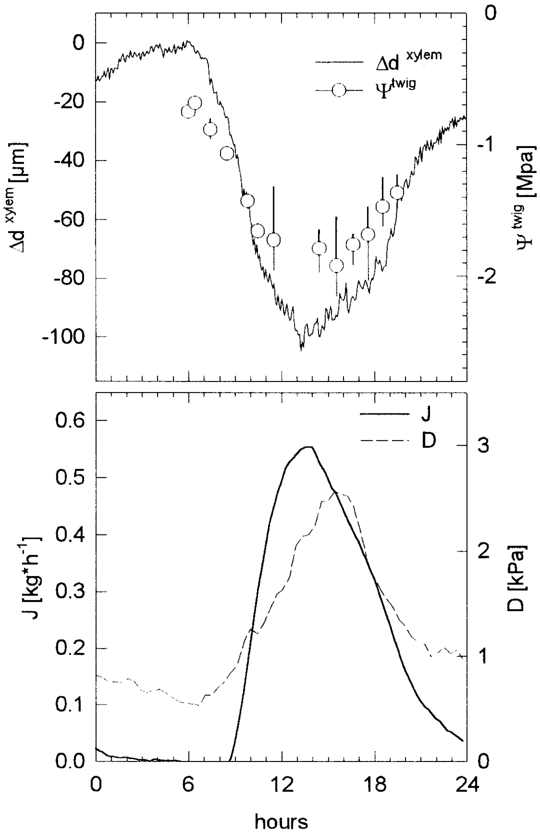

Fig. 2 Changes in wood diameter (*Δd*^{xylem}) at 13.7 m height of a Norway spruce tree, twig water potential (*Ψ*^{twig}) (error bars represent minimum/maximum values), sap flow (*J*) and day course of vapor pressure deficit (*D*) on 19 August 1998. The combination of low sap flow (usual range is 1.0–1.6 kg h^{-1} at peak flow) and large Δd^{xylem} (cf. DOY 231 in Fig. 4) corresponds to an increased hydraulic resistance between soil and the point where Δd^{xylem} was measured

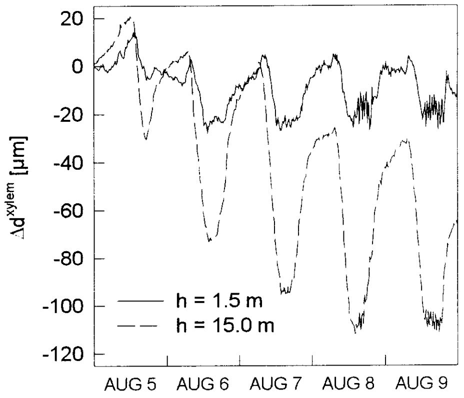

Fig. 3 Amplitude of diurnal changes in wood diameter (*Δd*^{xylem}) measured at different stem heights of a Norway spruce tree. Changes just below the crown (15.0 m) are far more pronounced than those at the stem base (1.5 m)

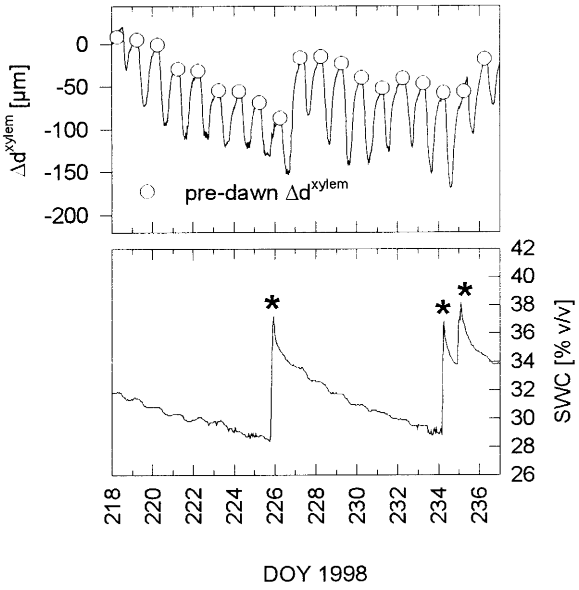

Fig. 4 Relation between changes in wood diameter (*Δd*^{xylem}) of Norway spruce and soil water content (*SWC*). Soil drought leads to decreasing pre-dawn values of Δ*d*^{xylem} (*open circles*) measured at 13.9 m stem height. After rainfall events (*asterisks*), pre-dawn Δ*d*^{xylem} rose rapidly together with soil water content

Table 1 Cross-correlation statistics of a time series of vapor pressure deficit (*D*), sapflow (*J*) and xylem diameter changes at 1.5 m (*Δd*^{xylem}) of Norway spruce (*lag [min]* minimum-mean-maximum lag in minutes relative to Δ*d*^{xylem} at the upper measuring position, *n* number of analysed day courses, r^2 mean correlation coefficient)

Tree	Parameter	*D*	*J*	Δ*d*^{xylem}
1	lag [min] n/r^2	0-0-0 8/0.842	0-0-15 8/0.937	5-45-110 23/0.876
2	lag [min] n/r^2	0-0-0 5/0.961	15-35-60 6/0.959	n.a.

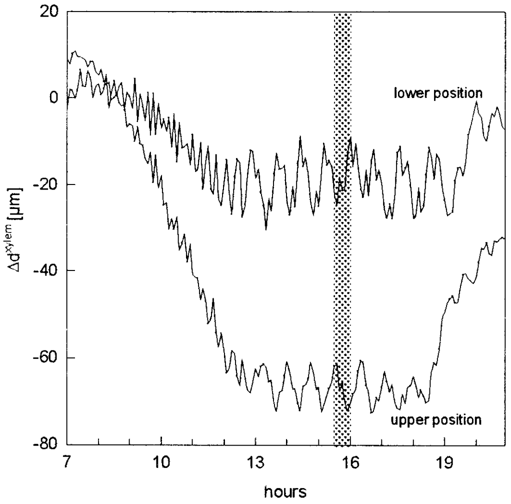

Fig. 5 Oscillation in wood diameter (Δd^{xylem}) measured at two different heights on 9 August 1998 (DOY 221). The oscillation has the same frequency but nearly opposite phase (indicated by the *grey bar*) between the upper (13.9 m) and lower (1.5 m) measuring positions

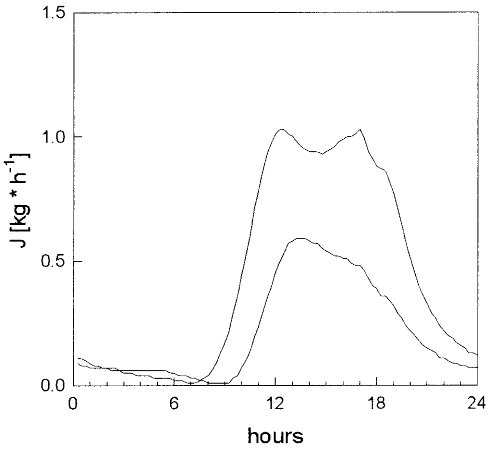

Fig. 6 Sap flow (*J*) at 2 m stem height on opposite sides of a Norway spruce on a day when oscillation in wood diameter was observed (9 August 1998). Note the aberrant flow pattern (two peaks) on the stem side with the higher flow rate

On a few occasions, conspicuous oscillation in wood diameter was observed around noon. The oscillation, which persisted for up to 5 h, was of smaller amplitude (about 10 µm) than the main diurnal cycle and had a period length of about 50 min (Fig. 5). Oscillations at different stem heights had the same frequency but were not in phase. The oscillation was observed on cloudless, warm days towards the end of a period of severe soil drought (compare DOY 220, 221, 223 and 225 in Fig. 4). On the days when oscillation occurred, sap flow on one side of the trunk showed two distinct peaks (Fig. 6), which is an anomalous pattern for spruce growing on that site.

Discussion

Whereas many authors hold that daily stem diameter variation is mainly or exclusively a result of phloem shrinkage (e.g. Molz and Klepper 1972; Molz et al. 1973; Parlange et al. 1975; Panterne et al. 1998), we found substantial xylem shrinkage and swelling in accordance with the results of Irvine and Grace (1997). Daily xylem diameter variation was in the range of changes reported for whole stems, including phloem and bark (Table 2). Xylem diameter change was always greater at the upper measurement point. A similar increase in amplitude with height has been reported for changes of stem circumference (Hinckley and Bruckerhoff 1975) and is the result of frictional water potential losses (Richter 1973), which lead to increasing water potential fluctuation (Legge and Connor 1985) and hence xylem diameter variation along the hydraulic pathway. Based on the simultaneous measurement of $\Delta d^{\mathrm{xylem}}$ and Ψ^{xylem}, we calculated the elastic modulus E_{r} for the radial contraction of sapwood at the higher stem position of tree no. 2. The definition of the elastic modulus E can be written in the trivial form:

$$E=\text{stress}*\text{strain}^{-1} \tag{1}$$

Replacing stress with xylem water tension and strain with the radial sapwood deformation relative to initial sapwood thickness, we arrive at:

$$E_{\mathrm{r}}=\Delta\Psi^{\mathrm{xylem}}*\Delta d^{\mathrm{xylem}-1}*\text{sapwood thickness} \tag{2}$$

from which we calculated an elastic modulus of E_{r} = 0.83 GPa. This is slightly higher than that found by Irvine and Grace (1997) for *Pinus sylvestris* (0.68 and 0.79 GPa for radial deformation under tension and pressure, respectively). This calculation contained the underlying assumption that only sapwood contributes to the observed change. The absence of significant diameter change in the heartwood was demonstrated in the experiments of Irvine and Grace (1997) and is evident from the fact that deforming water tensions can only build up in functional xylem conduits.

The living wood rays contribute only a small fraction to total sapwood volume (maximal 5.5% for Norway spruce; Wagenführ and Scheiber 1985) and both living cells and tracheids of spruce xylem have lignified walls and will shrink with increasing water tension. Thus the determination of a bulk elastic modulus for the whole sapwood seems justified.

Rewriting Eq.2 in the form of:

$$\Delta\Psi^{\mathrm{xylem}}=E_{\mathrm{r}}*\Delta d^{\mathrm{xylem}}*\text{sapwood thickness}^{-1} \tag{3}$$

seems to offer a very convenient way to calculate changes in xylem water potential from dendrometrical data. However, it is inappropriate to rely on a single determination of E_{r}, as the elasticity of wood shows substantial intra- and interspecific variation and will depend on the microfibril angle (Reiterer et al. 1999; Lichtenegger et al. 2000) and lignification of the cell walls, as well as the ra-

Table 2 Daily changes in stem diameter calculated from the literature. For clearer comparison of the data, the diameter changes were standardized. Relative change [ppm] = diameter change×10^6/diameter

Reference	Species	Absolute change (μm)	Relative change (ppm)	Originally cited as
Daum 1967	*Fraxinus pennsylvanica*	57[a]	106	Stem circumference
Daum 1967	*Fraxinus pennsylvanica*	64	118	Stem circumference without phloem and bark
Hinckley and Bruckerhoff 1975	*Quercus alba*	32–223	106–743	Stem circumference
Lassoie 1979	*Pseutotsuga menziesii*	29–255	72–636	Basal area
This report	*Picea abies*	10–30[b]	25–76	Stem diameter without phloem and bark
50–120[c]	267–642			

[a] Stem circumference was measured in 1964, circumference without phloem and bark in 1965 on the same tree

[b] At 1.5 m stem height

[c] At 15 m stem height

tio of early to late wood and other parameters which may vary even at different heights on the same stem. Figure 1 also shows deviation from the linear relationship between stem water potential and wood diameter in the early morning and at noon. Such a rapid change in E_r at first resembles an effect of cavitation (noon) and refilling (morning hours) of xylem conduits. However, the water potential (approximately –1.9 MPa) at which E_r apparently changed did not induce significant embolism in the xylem of conifer branches in other studies (Cochard 1992; Sperry and Ikeda 1997). In addition, one would expect a cavitating conduit to expand upon release of tension, leading to a bulk diameter increase rather than the further shrinking seen in Fig. 1. The development of a radial gradient in Ψ^{xylem} together with the limited measuring depth of the psychrometer attached to the xylem surface seems to be the most plausible explanation.

The fact that there was no apparent time-lag between D, Ψ^{twig} and xylem diameter at the upper dendrometer shows that a change in Ψ^{twig} resulting from transpiration was rapidly propagated towards the crown base. Apparently the crown had only a negligible storage capacity to buffer the decrease in Ψ^{twig}. Low values for canopy water storage (4% of total water storage) have been reported by Running (1979) for small individuals (2.7–8 m) of *Pinus contorta*. The contribution of canopy water storage to stand transpiration was even smaller for larger trees (0.1% for 50- to 60-m-high *Pseudotsuga menziesii*; Waring and Running 1978). Along the stem, the lower dendrometer lagged behind the upper one by up to 110 min, which is an additional indication that the bulk of capacitive water is stored in the bole and not in the crown. Delays between transpiration and whole-stem circumference have been observed before and were used to estimate (e.g. Simmoneau et al. 1993) and locate (Parlange et al. 1975; Milne 1989) the internal water resources of the tree. Thus what was considered previously to be a mere consequence of volume changes in the living tissues outside the cambium now appears to include a major contribution by the sapwood. A comparison of diameter variation measured with different methods (Table 2) exemplifies this.

Pre-dawn wood diameter, at least of the upper stem, reflected soil water content. During several prolonged periods without rain, wood diameter decreased but rapidly recovered to pre-drought values when soil water was replenished by rainfall. The pre-dawn ψ^{xylem} is assumed to be the water potential a plant reaches overnight by equilibration with soil water potential (for a critical review, see Sellin 1999) and is an important parameter for studies of plant water relations, often used as a measure of plant-available soil water. According to Sellin (1999), soil water availability accounted for 77% of the variation in base water potential (least negative water potential observed in 24 h) measured on shoots of Norway spruce trees. If the correlation between xylem diameter and ψ^{xylem} holds, pre-dawn diameter would be an equally useful parameter but much easier to measure over extended periods. Rapid expansion of the whole-stem diameter after rainfall was also observed by Herzog et al. (1995) for *Picea abies*; pre-dawn Ψ^{twig} and stem circumference at 07:00 hours in *Quercus alba* decreased during a dry period (Hinckley and Bruckerhoff 1975). The whole-stem diameter, however, can hardly be used as a measure of pre-dawn ψ^{xylem} over extended periods, because radial growth and osmotic adaptation of the phloem tissues would make it very difficult to establish a clear pressure-diameter relationship. As soil drought continued and D increased, pre-dawn values of $\psi^{*\mathrm{xylem}}$ (xylem water potential as inferred from wood diameter) fell even below the mid-day values found some days earlier. For this tree, E_r was not determined separately but can reasonably be assumed to fall in the range between 0.68 GPa (for Scots pine; Irvine and Grace 1997) and 0.83 GPa (determined for the other spruce at 15 m). Based on these values for E_r, the overall decline in pre-dawn stem diameter at the upper measuring position corresponded to a decrease in $\Psi^{*\mathrm{xylem}}$ of at least 0.76 MPa. During this time, bulk Ψ^{soil} in the rooting zone (calculated from soil water content at 20 cm depth) declined by only 0.095 MPa (H. Schume, personal communication). Consequently, the gradient between soil water potential and $\Psi^{*\mathrm{xylem}}$ at 13.7 m increased, which suggests a net depletion of plant internal water reserves. Under such circumstances one could expect, even under non-transpiring conditions, that resaturation of plant tissues gives rise to nocturnal sap flow. We did not, however, observe substantial sap-flow during the night. As the drought period continued, daily sap-flow maxima declined while the amplitudes of $\Delta d^{\mathrm{xylem}}$ became larger. This indicates a growing hydraulic resistance between the soil and the point where $\Delta d^{\mathrm{xylem}}$ was measured (13.7 m). Our data do not allow location of the origin of this increased resistance, but different mechanisms are possible: increased resistance in the bulk soil due to air-filled pores or at the soil-root interface as a result of shrinkage of the loamy soil, altered permeability of the root (Steudle and Peterson 1998), or a reduction in xylem conductivity resulting from emboli (Tyree and Dixon 1986; Brodribb and Hill 2000).

The most unexpected result was the regular oscillation of xylem diameter measured on one tree. The fact that this was observed only on some days but never at night and that the oscillation had different phases at two heights exclude a measurement artefact. Oscillation of stomatal aperture and consequently of transpiration and leaf water potential has been known for a long time (see Barrs 1971). Such changes result from an instability of the negative feedback control of stomatal activity and are often triggered by a step change in environmental conditions (Barrs 1971) which disturbs the steady-state of hydraulic flow (Naidoo and von Willert 1994). Lang et al. (1969) reported oscillation of Ψ^{xylem} in the petioles of cotton leaves and proposed Ψ^{xylem} as the synchronizing factor for otherwise randomly distributed (Stalfelt 1929) oscillation of the width of single stomata. Passioura and Tanner (1985) showed also that the hydraulic conductance of the root system can be induced to oscillate by a sudden change in air humidity. In our study, oscillation of stem diameter was observed only on warm, cloudless days at low soil water content. On such days, leaf water supply was very probably restricted, which has been recognized as a prerequisite for oscillation of leaf water balance by different authors (Florell and Ruffelt 1960; Barrs and Klepper 1967; Cox 1968).

We arrive at three possible explanations for the oscillation in stem diameter: (1) cyclic changes in stomatal aperture or (2) root conductivity, (3) redistribution of water between different trunk sectors. In the first case, the majority of stomata in the canopy must have experienced some synchronizing stimulus. Since Ψ^{twig} within the crown differed by at least 0.3 MPa over a height of about 10 m, with the single branches exposed to differing light intensities, stomatal reactions could not possibly be triggered by a uniform threshold but rather by a rapid change in leaf water potential. The absence of any significant delay between *D* and $\Delta d^{\mathrm{xylem}}$ shows that changes in leaf water potential propagated fast enough to ensure that changes in Ψ^{xylem} at the crown base could have a synchronizing effect on stomatal regulation in the whole crown. This in turn would feed back on Ψ^{xylem}, amplifying initially small fluctuations. On days when oscillation in stem diameter was observed, diurnal sap flow on one side of the stem showed a marked reduction during the mid-day hours, resulting in two distinct peaks in the morning and in the afternoon. While a similar depression frequently occurs in different species, it was a very unusual, seldom-observed sap flow pattern in the 10 spruce trees on which sap flow was monitored during the entire vegetation period. Sap flow on the opposite side of the stem showed the ‘normal’ shape with one peak, but was only half as high. This observation indicates serious differences in internal flow dynamics at close distance, whereas the stable progression of irradiation and *D* during the oscillation period suggests there was no external trigger involved.

Alternatively, the stem diameter oscillation could have been related to oscillation in root conductance. Unfortunately, no independent estimates of stomatal or root conductance were made during this period.

The third hypothesis (redistribution of water between different trunk sectors) was stimulated by the observation that sap flow rates, and with them presumably also Ψ^{xylem}, differed strongly between the two stem sides. A critical xylem water tension reached at noon could have led to a sudden redirection of water between the major pathways of stem sap flow, relaxing one sector of the sapwood while imposing more tension onto the other. This could have initiated a series of tension-expansion cycles which appeared as measurable oscillation.

Our conclusion from these results is that change in wood diameter gives a more accurate estimate of xylem water potential than measurement of whole-stem circumference. Measurement of wood diameter is not biased by radial growth. Further, it excludes the time-lag introduced by radial water movement during equilibration of phloem and xylem water potentials, but includes the capacitive effect of phloem water storage on Ψ^{xylem}. This is of particular importance when sap flow and longitudinal gradients of Ψ^{xylem} are used to calculate the time constant for water exchange between phloem tissues and the transpiration stream. The experimental setup is robust and requires little maintenance, which makes it an appropriate tool for field studies. Interpretation of results is limited to a description of the general trend of xylem water potential, unless the elastic modulus of the specific sample can be determined by independent measurements of Ψ^{xylem}. However, this relative trend as such contains valuable information about the long-term development of tree water status, as became evident during periods of soil drought and rewetting.

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References

Barrs HD (1971) Cyclic variations in stomatal aperture, transpiration and leaf water potential under constant environmental conditions. Annu Rev Plant Physiol 22:223–236

Barrs HD, Klepper B (1967) Cyclic variations in plant properties under constant environmental conditions. Physiol Plant 21: 711–730

Bode HR (1923) Beitraege zur Dynamik der Wasserbewegung in den Gefaesspflanzen. Jahrb Wiss Bot 62:93–127

Brodribb TJ, Hill RS (2000) Increases in water potential gradient reduce xylem conductivity in whole plants. Evidence from a low-pressure conductivity method. Plant Physiol 123:1021–1028

Brough DW, Jones HG, Grace J (1986) Diurnal changes in water content of the stems of apple trees, as influenced by irrigation. Plant Cell Environ 9:1–7

Cochard H (1992) Vulnerability of several conifers to air embolism. Tree Physiol 11:73–83

Cox EF (1968) Cyclic changes in transpiration of sunflower leaves in a steady environment. J Exp Bot 19:167–75

Daum CR (1967) A method for determining water transport in trees. Ecology 48:425–431

Dixon MA, Tyree MT (1984) A new stem hygrometer, corrected for temperature gradients and calibrated against the pressure bomb. Plant Cell Environ 7:693–697

Čermák J, Deml M, Penka M (1973) A new method of sap flow rate determination in trees. Biol Plant 3:171-178

Florell C, Ruffelt H (1960) Transpiration of wheat plants cultivated under different environmental conditions. Physiol Plant 13: 482–86

Friedrich J (1897a) Über den Einfluß der Witterung auf den Baumzuwachs. Mitteilungen aus dem forstlichen Versuchswesen Österreichs, vol 21. K.K. Forstliche Versuchsanstalt, Mariabrunn, Austria

Friedrich J (1897b) Über den Einfluß der Witterung auf den Baumzuwachs. Centralbl Gesammte Forstwes 23:470–495

Haasis FW (1934) Diametral changes in tree trunks. Publication 450. Carnegie Institute, Washington, D.C.

Herzog KM, Häsler R, Thum R (1995) Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration. Trees 10:94–101

Hinckley TM, Bruckerhoff DN (1975) The effects of drought on water relations and stem shrinkage of *Quercus alba*. Can J Bot 53:62–72

Irvine J, Grace J (1997) Continuous measurements of water tensions in the xylem of trees based on the elastic properties of wood. Planta 202:455–461

Lang ARG, Klepper B, Cumming MJ (1969) Leaf water balance during oscillation of stomatal aperture. Plant Physiol 44:826–830

Lassoie JP (1979) Stem dimensional fluctuations in Douglas-fir of different crown classes. For Sci 25:132–144

Lax E (1967) In: D'Ans J, Lax E (eds) Handbuch für Chemiker und Physiker, 3rd edn, vol I. Springer, Heidelberg Berlin New York

Legge NJ, Connor DJ (1985) Hydraulic characteristics of mountain ash (*Eucalyptus regnans* F. Muell.) derived from in situ measurements of stem water potential. Aust J Plant Physiol 12:77–88

Lichtenegger H, Reiterer A, Stanzl-Tschegg SE, Fratzl P (2000) Microfibril angle and mechanical properties of wood. In: Spatz HC, Speck T (eds) Plant biomechanics 2000. Thieme, Freiburg, Germany, pp 436–42

Lövdahl L., Odin H. (1992) Diurnal changes in the stem diameter of Norway spruce in relation to relative humidity and air temperature. Trees 6:245–251

Milne R (1989) Diurnal water storage in the stems of *Picea sitchensis* (Bong.) Carr. Plant Cell Environ 12:63–72

Molz FJ, Klepper B (1972) Radial propagation of water potential in stems. Agron J 64:469–473

Molz FJ, Klepper B, Browning VD (1973) Radial diffusion of free energy in stem phloem: an experimental study. Agron J 65:219–222

Naidoo G, von Willert DJ (1994) Stomatal oscillations in the mangrove *Avicennia germinans*. Funct Ecol 8:651–657

Panterne P, Burger J, Cruiziat P (1998) A model of the variation of water potential and diameter within a woody axis cross-section under transpiration conditions. Trees 12:293–301

Parlange J-Y, Turner NC, Waggoner PE (1975) Water uptake, diameter change, and nonlinear diffusion in tree stems. Plant Physiol 55:247–250

Passioura JB, Tanner CB (1985) Oscillations in apparent hydraulic conductance of cotton plants. Aust J Plant Physiol 12:455–61

Reiterer A, Lichtenegger H, Tschegg S, Fratzl P (1999) Experimental evidence for a mechanical function of the cellulose microfibril angle in wood cell walls. Philos Mag A79:2173–84

Richter H (1973) Frictional potential losses and total water potential in plants: a re-evaluation. J Exp Bot 24:983–94

Running SW (1979) Environmental and physiological control of water flux through *Pinus contorta*. PhD thesis, Colorado State University, Fort Collins, Colo, USA

Sellin A (1999) Does pre-dawn water potential reflect conditions of equilibrium in plant and soil water status? Acta Oecol 20:51–59

Simmoneau T, Habib R, Goutouly J-P, Huguet J-G (1993) Diurnal changes in stem diameter depend upon variations in water content: direct evidence in peach trees. J Exp Bot 44:615–621

Sperry JS, Ikeda T (1997) Xylem cavitation in roots and stems of Douglas-fir and white fir. Tree Physiol 17:275–280

Stalfelt MG (1929) Pulsierende Blattgewebe. Planta 7:720–34

Steudle E, Peterson CA (1998) How does water get through roots? J Exp Bot 49:775–788

Tyree MT, Dixon MA (1986) Water stress induced cavitation and embolism in some woody plants. Physiol Plant 66:397–405

Wagenführ R, Scheiber C (1985) Holzatlas, 2nd edn. VEB, Leipzig

Waring RH, Running SW (1978) Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Environ 1:131–140

Wronski EB, Holmes JW, Turner NC (1985) Phase and amplitude relations between transpiration, water potential and stem shrinkage. Plant Cell Environ 8:613–622