BOREAL ENVIRONMENT RESEARCH 10: 447–458 ISSN 1239-6095
Helsinki 24 October 2005 © 2005

Relationships between diurnal xylem diameter variation and environmental factors in Scots pine

Sanna Sevanto[1)]*, Teemu Hölttä[1)], Tiina Markkanen[1)], Martti Perämäki[2)], Eero Nikinmaa[2)] and Timo Vesala[1)]

[1)] *Department of Physical Sciences, P.O. Box 64, FI-00014 University of Helsinki, Finland*
[2)] *Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland*
* *Present address: Harvard University, Department of Organismic and Evolutionary Biology, 3105 BioLabs, 16 Divinity Avenue, Cambridge, MA 02138, USA*

Sevanto, S., Hölttä, T., Markkanen, T., Perämäki, M., Nikinmaa, E. & Vesala, T. 2005: Relationships between diurnal xylem diameter variation and environmental factors in Scots pine. *Boreal Env. Res.* 10: 447–458.

We analyzed the variability in diurnal xylem diameter in Scots pine (*Pinus sylvestris*) by comparing daily maximum, minimum and average diameters and daily amplitudes of variation with environmental variables related to transpiration and water uptake from the soil. The measurements were carried out during six summers, 1999–2004 at SMEAR II station in Hyytiälä, southern Finland. We found that the daily maximum, minimum and average diameters and amplitudes were closest related to daily average water vapor deficits (VPD) and soil water contents in A-horizon (θ_A). However, the highest degree of determination was only 37%. That was found for daily minimum diameter by VPD. The degree of determination and correlation could be improved by making up variables that took into account the variation in factors related to transpiration and soil water availability. In that case the highest correlation (negative correlation) and coefficient of determination was found for daily minimum diameter by VPD scaled with θ_A so that VPD was enhanced when soil water content was low ($VPD^* = VPD^*(\theta_{Amin}/\theta_A)$). This could explain 50% of the variation in daily minimum diameters. The results emphasize the importance of both inflow- and outflow-related factors in explaining the water tension and water status of tree stems.

Introduction

Trees are the main transporters of water from the soil to the atmosphere in forest-covered areas. When water is freely available, summertime transpiration can reach 5–10 kg m^{-2} day^{-1} (Waring and Schlesinger 1985, Markkanen *et al.* 2001, Pilegaard *et al.* 2003). Transpiration can be seen as a consequence of stomatal opening for carbon intake to be used in photosynthesis. Thus, transpiration rate is determined by the aperture of stomata and the water vapor concentration gradient between the air in a stoma and the surroundings. In addition to the weather conditions, the aperture of stomata is affected by the feasibility of water uptake from the soil. During drought water is more tightly bound to soil and higher tension at leaf is needed to maintain similar flow rate. However, there is a maximum tension that can develop in leaves until a runaway embolism would render xylem non-functional (Tyree and Sperry 1989).

Tree stem diameter varies diurnally as a result of transpiration induced tension in the sap (Irvine and Grace 1997). The diameter is largest just before sunrise in the morning and smallest in the early afternoon when transpiration rates are highest. Xylem diameter variations are exceedingly closely linked with transpiration (Herzog *et al.* 1995, Perämäki *et al.* 2001). Even the small variations in transpiration rates (and thus water tension) due to changes in cloud cover are observable in the xylem diameter. The daily amplitude of the variation is determined by the daily maximum transpiration rate, soil water availability (Perämäki *et al.* 2001), and the dimensions and properties of the stem (Sevanto *et al.* 2003, Perämäki *et al.* 2005). The higher the transpiration rate the higher the water tension and larger the amplitude. Absence of transpiration or no resistance of water flow from the soil through the stem results in zero amplitude. Drying or wetting of the soil can also be seen in the overall trend of the stem diameter. After rainfall stems tend to swell and during dry periods they shrink. This overall pattern is best observed in the maximum values of diameter just before sunrise (Sevanto *et al.* 2001).

In this study we compared xylem diameter variations of Scots pine (*Pinus sylvestris*) with environmental factors driving transpiration or limiting water uptake. The aims of this study were to determine (I) how well the interannual variability of the determinants of stem water content are reflected in xylem diameter and (II) what factors contribute most to the overall variations in the xylem diameter. As driving and limiting factors we used the soil water content (θ), soil water tension (ψ), photosynthetically active radiation (PPFD), water vapor deficit (VPD), water vapor flux (F_w) and bulk canopy conductance (g_b).

Material and methods

The measurements were carried out during summers 1999–2004 at SMEAR II station in Hyytiälä, southern Finland (61°51´N, 24°17´E). The station is located in a Scots pine stand 181 m above sea level. The stand was established in 1962 through direct sowing after clear felling and prescribed burning. The dominant trees are approximately 15 m tall and the median diameter at breast height is 15 cm. Species other than Scots pine are downy birch (*Betula pubescens*), grey alder (*Alnus incana*) and European aspen (*Populus tremula*), but they represent only 1% of the biomass. The soil is podzolic and composed of sandy and coarse silty glacial till. The ground vegetation is dominated by heather (*Calluna vulgaris*), lingonberry (*Vaccinium vitis-idaea*) and blueberry (*V. myrtillus*) and the dominant moss species is wavy dicranum (*Dicranum polysetum*). The annual mean temperature in 1961–1990 was 2.9 °C and precipitation 709 mm. All-sided leaf area index (LAI) was 8 in years 1999–2001. Between January and March 2002 part of the stand was thinned and LAI in the thinned area dropped from 8 to 6. This did not, however have any effect on the surface fluxes of the canopy (Vesala *et al.* 2005).

Water vapor flux was measured with the eddy covariance technique, a method to determine the exchange rate of a compound across the interface between the atmosphere and a plant canopy (*see* e.g. Markkanen *et al.* 2001). The wind speed, needed for this analysis, was measured by two sonic anemometers from two different towers: Solent Research 1012R2 (Tower 1) and Solent Research 1199HS (Tower 2) (Gill Instruments Ltd., Lymington, Hampshire, England). The towers were located close to each other in the same stand and data from one could be used to fill possible gaps in the data series from the other. The measurements were carried out at a height of 23 m, approximately 10 m above the forest canopy. The water vapor concentration was measured with an infrared absorption gas analyzer Li-6262 (LI-COR Inc., Lincoln, NE, USA). The collected data quality was controlled and corrected for frequency losses and sensor separation in a standard way (Rannik 1998, Aubinet *et al.* 2000, Buzorius 2000) and averaged to give half-hourly flux values. Data collected during low friction velocity (u*) episodes (below 0.3 m s^{-1}) were omitted due to possible underestimation of the fluxes (Vesala *et al.* 2005).

Xylem diameter variations were measured using LVDTs (linear displacement transducer; Solartron AX/5.0/S; Solartron Inc., West Sussex, UK). The sensors were attached to rigid metal frames consisting of four metal bars forming a rectangle around the stem. In order to detect variations of the xylem diameter, two screws were screwed on opposite sides of the stem and the sensor tip was placed on one, and the frame bar opposite the sensor on the other. The screws enabled us to detect xylem diameter variations only and thus growth of the stem was not a concern. The whole frame was attached to the stem using metal plates and screws about 15 cm above the measuring height. The measurement frequency was 0.2 min^{-1} in 1999 and 1 min^{-1} in 2000–2004. The temperature of the frame was measured with a copper-constantan thermo-couple and the correction for the combined effect of thermal expansion of the frame and wood was made using a coefficient of thermal expansion of 15.8×10^{-6} $°\text{C}^{-1}$ for the frame and 7.9×10^{-6} $°\text{C}^{-1}$ for the wood (for a more detailed description, *see* Sevanto *et al.* 2005). The xylem diameter variation was detected on different trees every year, but the measurement height was kept at 1.5–2.0 m. In 1999–2003 the sensors were on one tree and 2004 on two. The diameters of the trees at the measurement height varied between 15 and 19 cm. The trees that grew closer than 20 m apart were selected among the dominants of the stand whose contribution to the total ecosystem water cycle would be significant. Sevanto *et al.* (2001) reported similar xylem diameter variation measurements from four different Scots pine trees (diameters 8–20 cm) at the experimental site used in this study. Their results showed that all the trees responded similarly and simultaneously to variations in stem water balance (that is, changes in stem water tension). The only slight differences (< 10%) among individuals were observed in the amplitude of diameter variation, which is related to the amount and elastic properties of sapwood, the elastic contracting tissue. Thus the xylem diameter of individual healthy trees in the same stand can be said to respond similarly to varying environmental conditions.

The volumetric liquid soil water content was measured with time-domain reflectometry (TDR) in the humus layer and A- B- and C-horizons with Tektronix 1502C cable radar (Tektronix Inc., Redmond, WA). The depths of the layers were humus 0–5 cm, A-horizon 5–9 cm and B-horizon 9–34 cm. Soil water content data was collected only during summers 1999–2003.

For A-horizon, soil water content values (θ [$\text{m}^3\ \text{m}^{-3}$]) were converted to water tensions (ψ) by separately determined soil water retention curves (*see* Mecke *et al.* 2000 and Mecke *et al.* 2002). The relationship (ψ [kPa]) found was

$$\psi = -22344e^{-20.244\theta}. \qquad (1)$$

The curve explained 97% of the observations at our site.

Photosynthetically active photon flux density (PPFD) was measured above the canopy level from a tower using a quantum yield sensor (Li-Cor LI-190 SZ, Li-Cor Inc., Lincoln, Nebraska, USA). Relative humidity was calculated from water vapor concentration and air temperature measurements. Water vapor concentration was measured with an infrared light absorption analyzer (URAS 4 H2O, Hartmann & Braun, Frankfurt am Main, Germany) at 8.4 m height. In air temperature measurements PT-100 resistance thermometers, which are protected from solar radiation and ventilated by fans, were used at a height of 8.4 m. Half-hourly precipitation was measured above the canopy level from a tower with an ARG-100 tipping bucket counter (Vector Instruments, UK).

In this study we analyzed data from summer periods only, which were defined to begin on 1 May and to end on 31 August, each year. To analyze for long-term variations we calculated daily maximum and minimum xylem diameters, daily average diameters and daily amplitudes of xylem diameter variation (= maximum diameter – minimum diameter) and compared them with daily averages of photosynthetically active photon flux density (PPFD), water vapor deficit (VPD), water vapor flux (F_w), bulk canopy conductance (g_b) and soil water contents (θ) for humus layer, A- and B- horizons and soil water tension (ψ) for A-horizon. The stem diameter was adjusted to zero in the beginning of the measurement period of each year. The bulk canopy conductance was calculated from water vapor flux as follows:

$$g_b = F_w/\text{VPD} \qquad (2)$$

where the unit of F_w is mol $\text{m}^{-2}\ \text{s}^{-1}$ and thus that

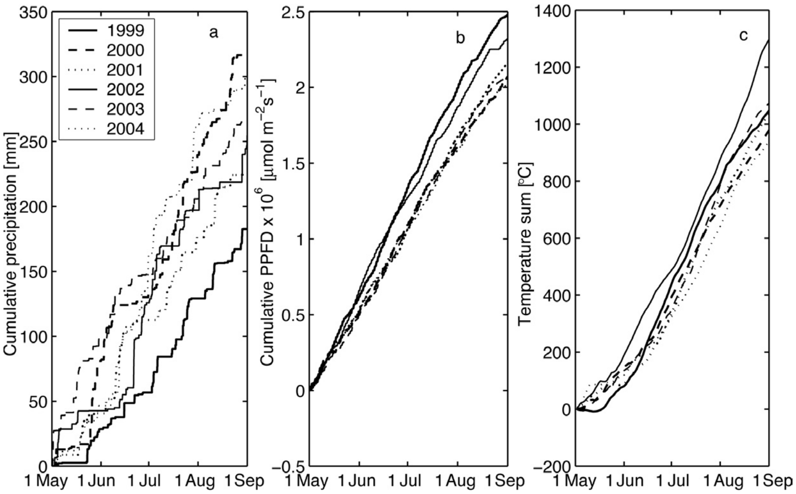

Fig. 1. (**a**) Cumulative precipitation, (**b**) cumulative photosynthetically active photon flux density (PPFD), and (**c**) temperature sum in summers 1999–2004.

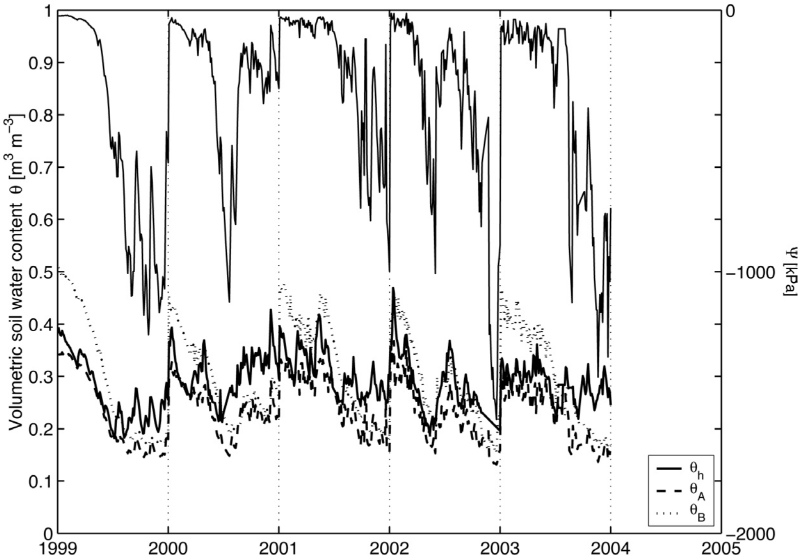

Fig. 2. Daily averages of volumetric soil water contents (θ) in humus layer (0–5 cm), A-horizon (5–9 cm) and B-horizon (9–34 cm) (thick lines), and soil water tension in A-horizon (thin line) in summers 1999–2004. Summer was defined to start on 1 May and end on 31 August. The gridlines mark the beginning of a new summer. The gap in 2004 is due to missing data.

of VPD is mol m^{-3}. When there is no evaporation on wet surfaces F_w represents transpiration and g_b can be used as an estimate for bulk canopy stomatal conductance (*see* e.g. Seinfeld and Pandis 1998). The statistical significance of the correlation coefficients, slopes and differences of averages were tested with Student's *t*-test and the significance limit was set to $p < 0.01$.

Results

Interannual variability in xylem diameter

Of the six summers used in this study summer 2000 was the wettest (total precipitation 316 mm) (Fig. 1). It was also among the lowest in total amount of radiation. Summer 1999 was the sunniest and driest with 183 mm rainfall. The warmest of all was summer 2002 with a total temperature sum of 1300 °C. All the other years had close to the same amount of radiation, the total amount of rainfall varied 25% (225–300 mm) amongst those years and the temperature sum was 940–1070 °C.

Timing of the rainfall events varied from year to year. Summer 2003 was the wettest during May and June, while 2000, with most precipitation, was among the driest ones in the beginning of the summer (Fig. 1a). These pat-

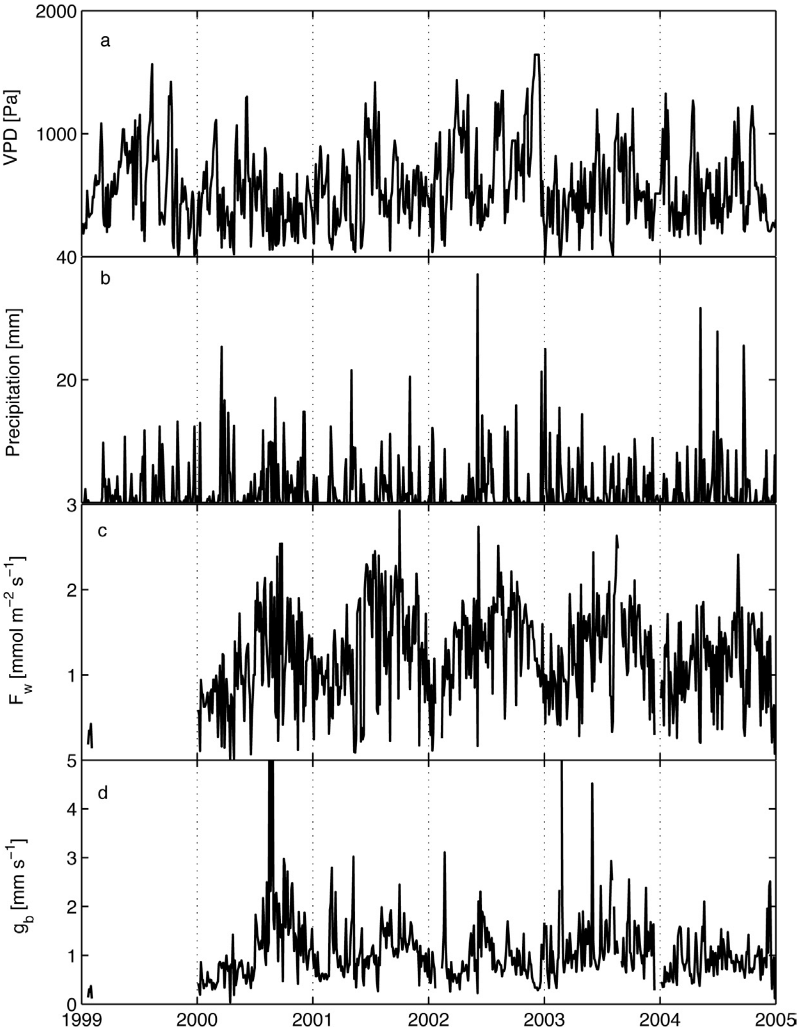

Fig. 3. The summer patterns of daily averages of (**a**) water vapor deficit (VPD), (**b**) precipitation, (**c**) water vapor flux (F_w), and (**d**) bulk canopy conductance (g_b) in summers 1999–2004. Summer was defined to start on 1 May and end on 31 August. The gridlines mark the beginning of a new summer. g_b was calculated from F_w by dividing by VPD and omitting very wet (RH > 70%) conditions.

terns were reflected in the soil water content, most profoundly in the humus layer and A-horizon (Fig. 2). However, deeper layers followed a yearly pattern of high water contents in the early summer drying out later, although the more severe droughts e.g. mid-summer 2000 and late May–early June and August in 2002 are visible also in deep soil layers.

The average evaporative demand was highest in summer 2002 (mean VPD 769 Pa) and lowest in summer 2003 (mean VPD 505 Pa) (Fig. 3a). However, the maximum VPD was almost the same in all the three warmest summers (1999, 2002 and 2003), and the low mean value in 2003 was due to the low VPD in early summer. The general pattern of VPD was a decrease towards the end of August every year with the exception of 2002 when the lowest VPD was in late August. The periods of high or low rainfall (Fig. 3b) were hardly visible in VPD data because at our site RH reaches 100% every summer night, except during long, severely dry periods. The water vapor flux showed a clear summer pattern peaking each year in late July (Fig. 3c). However, the bulk canopy conductance was quite constant throughout the summers (Fig. 3d) except in 2000, when there was a peak in July.

The daily xylem diameters showed a decreasing pattern in summers that dried towards the fall as in 2002 (Fig. 4). The pattern was opposite during wet periods (e.g. summer 2000 and late summer 2003). The daily maximums peaked

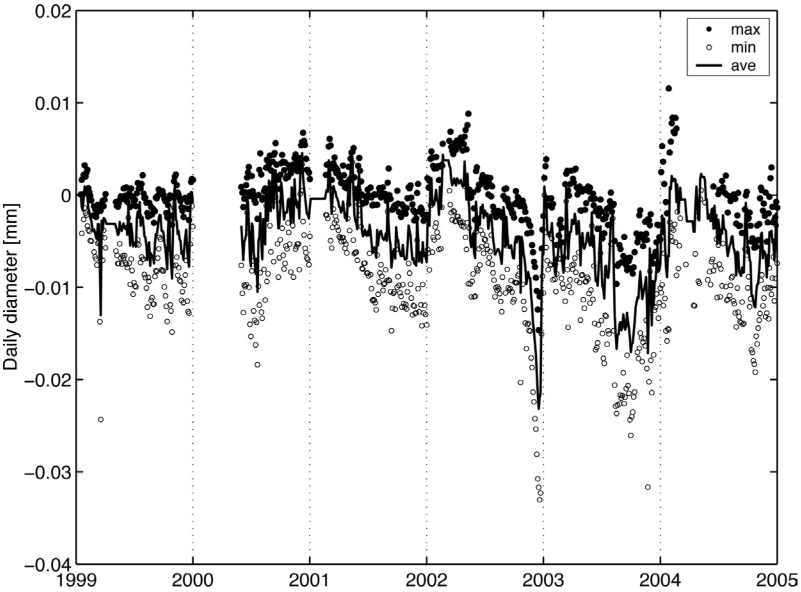

Fig. 4. Daily maximum, minimum and average xylem diameters for summers 1999–2004. Summer was defined to start on 1 May and to end on 31 August. The gridlines mark the beginning of a new summer. The diameter was adjusted to zero in the beginning of each summer when the soil water content was highest. The gap in 2000 is due to missing data.

during high precipitation (e.g. early summer 2002) and minimums dropped during dry periods. The amplitudes (maximum–minimum) seemed to increase during dry periods. The diameters during summers 1999 and 2002 that were highest in radiation and among the lowest ones in precipitation did not follow a similar yearly pattern. In 2002 there was a large shrinkage in the diameter towards the end of the summer while in 1999 the pattern was almost flat and resembled more closely that of 2001. This difference in the patterns may result from the difference in the timing of the rainfall. Summer 2002 was very wet in the beginning and very dry in late July and August (only 5 mm rainfall for 15 days), while summer 1999 was dry in the beginning and after that the precipitation rate was even. The lack of rainfall in early summer 1999 did not show in stem diameter since the soil water content was high after snow melting. We have assumed that the water reservoirs also in the stems were full in the beginning of each summer (i.e. we adjusted the stem diameter to zero in the beginning of each summer). That is well justified by the tendency of melt water to fill the soil water retention capacity in spring

Table 1. Correlation coefficients (C) and coefficients of determination (R^2) between basic environmental variables and daily averages of xylem diameter. PPFD values were taken for hours when the elevation angle of the sun was above –3° and the bulk canopy conductance, g_b, was calculated at RH < 70%. Statistically insignificant correlations are marked with n.s. and in those cases R^2 is not given. Coefficients with the same letter appearing in superscript do not differ statistically significantly ($p > 0.01$).

	Max. diameter		Min. diameter		Avg. diameter		Amplitude	
	C	R^2	C	R^2	C	R^2	C	R^2
PPFD	–0.042n.s.		–0.25	0.062	–0.19	0.036	0.35	0.10
VPD	-0.28^{a}	0.078	-0.45^{d}	0.20	-0.41^{cd}	0.17	0.43^{b}	0.18
F_w	-0.26^{a}	0.068	-0.34^{ac}	0.12	-0.33^{ac}	0.11	0.27	0.07
g_b	–0.006n.s.		–0.044n.s.		–0.030n.s.		–0.007n.s.	
θ_h	0.42^{b}	0.18	0.49^{br}	0.24	0.49^{br}	0.24	-0.40^{h}	0.16
θ_A	0.45^{br}	0.20	0.57^{s}	0.32	0.55^{s}	0.30	-0.51^{y}	0.26
θ_B	0.35	0.12	0.49^{br}	0.24	0.46^{br}	0.21	-0.47^{hy}	0.22
ψ	0.53^{sr}	0.28	0.60^{s}	0.36	0.60^{s}	0.36	-0.49^{y}	0.24

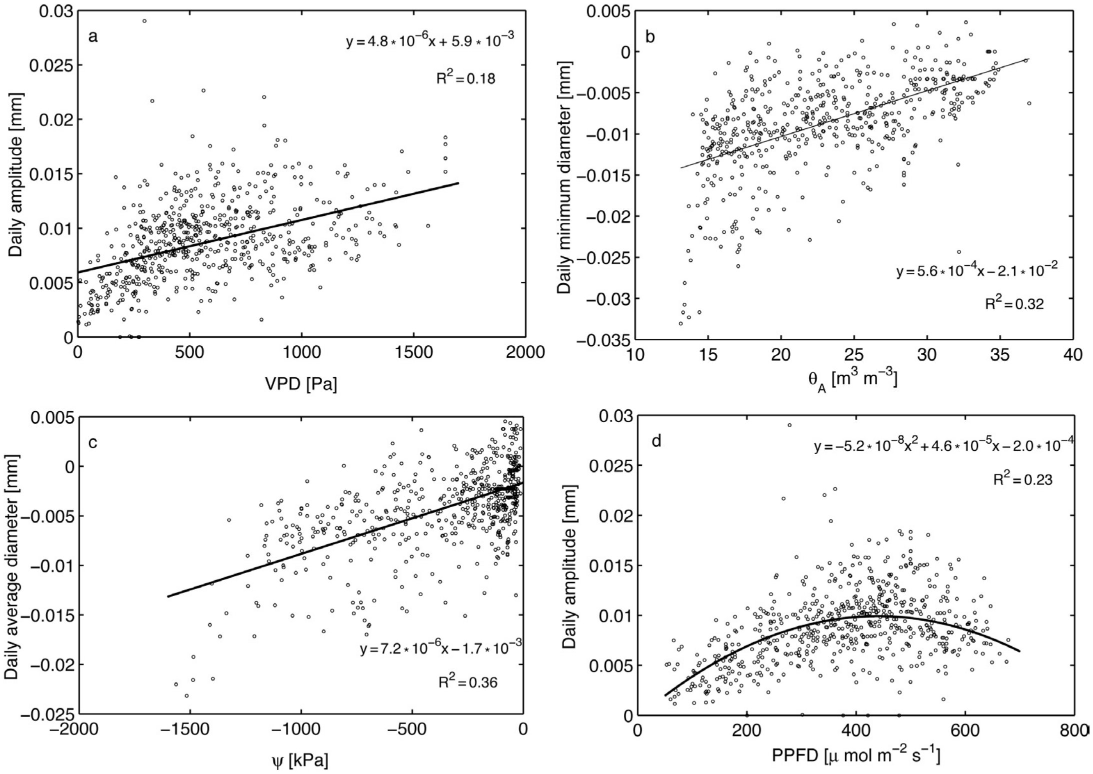

Fig. 5. Examples of relationships between daily averages of environmental variables and xylem diameter values. (**a**) water vapor deficit (VPD) versus daily amplitude, (**b**) volumetric soil water content of A-horizon (θ_A) versus daily minimum diameter, (**c**) Soil water tension (ψ) in A-horizon versus daily average diameter, and (**d**) photosynthetically active photon flux density (PPFD) versus daily amplitude of diameter variation. PPFD values are taken when the elevation angle of the sun > –3°. The regressions are calculated with the least-square method.

and the soil water content seems to be highest at the beginning of the analyzed period (Fig. 2). However, the stems seemed not to be at maximum water content at that time since the daily maximum and even the average xylem diameters reached above-zero values every summer. In spite of the clear differences in annual environmental conditions, no statistically significant differences were found between yearly averages of xylem diameter values (maximum, minimum, mean and amplitude).

Factors affecting long-term patterns in xylem diameter

A comparison of daily maximums and minimums of the xylem diameter with basic environmental variables showed that diameter values co-varied most closely with soil water contents and soil water tension (Table 1). The variations in the soil water content were slightly more correlated with the minimum and average diameters than with the maximum diameters. The water content of B-horizon, especially, showed lower correlation ($p < 0.001$) with the maximum diameters than with the others. In general, daily average diameters had correlations somewhere between maximum and minimum diameters, as could be expected, but their behavior was closer to minimum than maximum diameters. Daily amplitudes of diameter variation were best correlated with VPD, but θ and ψ gave higher coefficients of determination. The correlation type with these was negative correlation.

We applied a linear regression model (best model with two parameters; least-square type) to explain daily xylem diameter values by most of the basic environmental variables (e.g. Fig. 5a–c). However, the only statistically significant slopes were found for diameter values with θ_h, θ_A and ψ, and for maximum, minimum and average diameters with VPD. The trends of the maximum, minimum and average diameter values with the soil water contents were increasing, so that the diameter values were closest to zero at high soil water contents (all data not shown). However, the daily amplitude showed a decreasing trend with the increasing soil water content. With VPD the trends were opposite. The coefficients of determination were low. Highest explicability was found by ψ_A explaining 36% of variations in minimum and average diameters. Interestingly with PPFD, the daily amplitudes could be better explained by a nonlinear relationship (Fig. 5d). By applying a curvilinear (second order) model to that increased the explicability from 10% to 23%.

Since the co-variance and explicability of the variation in the xylem diameter by basic environmental variables was poor, we tried to find what combination of factors affecting the outflow and inflow of water in the stem could explain a higher amount of the variability. We combined variables related to factors affecting transpiration (PPFD, VPD, F_w and g_b) with θ from different depths (subscripts h, A and B) and with ψ_A. We used two scaling procedures: one that stressed the values of the variable when the soil water content was high and reduced them when the soil water content was low (e.g. PPFD* = PPFD × θ^*_A, where $\theta^*_A = \theta_{Amax} = \theta_A/\theta_A$ maximum), and one that reduced the values of the variable when the soil water content was high and enhanced them when the soil water content was low (in this case $\theta_{Amin} = \theta_A$ minimum/θ_A). Effectively, the first procedure thus evened up the driving force for transpiration and enhanced the availability of water replacement from the soil. The second, on the other hand, stressed the aspect of the water tension build-up by high transpiration rate versus soil water availability.

The highest coefficients for each combination are shown in Table 2. In general, scaled variables showed higher correlations and could explain more of the variation of daily diameter values than pure variables. In all cases except with ψ and g_b (not shown) the latter procedure gave higher correlation and better explicability than the first one. In the case of g_b the highest correlation came alternatively from the first or second procedure without any explainable reason. That reflected only the inability of this variable to explain the variation in the diameter values (highest R^2 obtained was 0.2). Scaling by θ_h was less successful than scaling by θ_A, θ_B or ψ. The largest improvement of explicability by scaling was achieved with F_w.

Daily maximum diameter could be best explained by VPD scaled by ψ_{Amax} or θ_{Bmin}, but

Table 2. Correlation coefficients (*C*) and coefficients of determination (R^2) between the combinations of environmental variables and daily averages of xylem diameter. The subscript max or min indicates the procedure of scaling that gave the highest correlation. θ_{min} = minimum θ/θ and $\theta_{max} = \theta$/maximum θ. PPFD values were taken for hours when the elevation angle of the sun was above –3° and the bulk canopy conductance, g_b, was calculated at RH < 70%. Coefficients with the same letter appearing in superscript do not differ statistically significantly ($p > 0.01$).

	Max. diameter		Min. diameter		Avg. diameter		Amplitude	
	C	R^2	*C*	R^2	*C*	R^2	*C*	R^2
PPFD × θ_{hmin}	–0.20	0.04	–0.39^{a}	0.15	–0.33^{a}	0.11	0.43^{f}	0.18
PPFD × θ_{Amin}	–0.33^{a}	0.11	–0.55^{c}	0.31	–0.50^{bc}	0.25	0.58^{fg}	0.34
PPFD × θ_{Bmin}	–0.32^{a}	0.10	–0.55^{c}	0.31	–0.49^{bc}	0.24	0.59^{fg}	0.35
PPFD × ψ_{max}	–0.50^{b}	0.25	–0.64^{de}	0.41	–0.62^{de}	0.38	0.58^{fg}	0.34
VPD × θ_{hmin}	–0.35^{a}	0.12	–0.48^{b}	0.23	–0.45^{ab}	0.20	0.45^{f}	0.20
VPD × θ_{Amin}	–0.45^{ab}	0.20	–0.59^{c}	0.35	–0.57^{c}	0.32	0.53^{fg}	0.28
VPD × θ_{Bmin}	–0.53^{bc}	0.28	–0.68^{e}	0.46	–0.66^{e}	0.44	0.60^{gh}	0.36
VPD × ψ_{max}	–0.54^{bc}	0.29	–0.64^{de}	0.41	–0.63^{de}	0.40	0.53^{fg}	0.28
$F_w \times \theta_{hmin}$	–0.31^{a}	0.10	–0.51^{c}	0.26	–0.45^{ab}	0.20	0.55^{f}	0.30
$F_w \times \theta_{Amin}$	–0.39^{a}	0.15	–0.60^{d}	0.36	–0.55^{c}	0.30	0.63^{h}	0.40
$F_w \times \theta_{Bmin}$	–0.37^{a}	0.14	–0.59^{d}	0.35	–0.53^{bc}	0.28	0.63^{h}	0.40
$F_w \times \psi_{max}$	–0.45^{ab}	0.20	–0.63^{de}	0.40	–0.59^{d}	0.35	0.60^{gh}	0.36

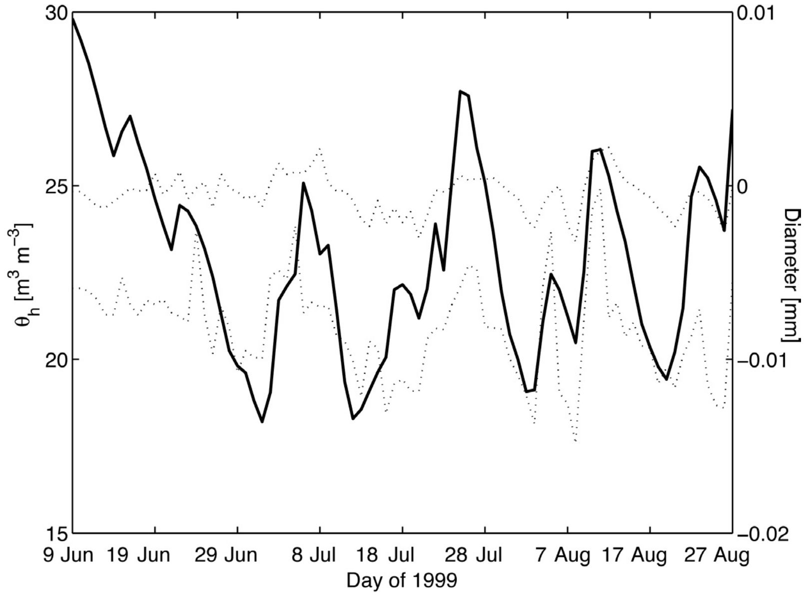

Fig. 6. An example of the period when both daily maximum and minimum diameters (thin dotted lines) follow the soil water content in the humus layer (thick solid line). The data is from summer 1999.

the correlation did not differ statistically significantly from those obtained for PPFD scaled by $\psi_{\max}$, VPD scaled by θ_{Amin} or F_{w} scaled by $\psi_{\max}$. For daily minimum diameter, VPD scaled by θ_{Bmin} gave the highest explicability, but again the coefficients obtained by scaling PPFD with $\psi_{\max}$, VPD with $\psi_{\max}$ or F_{w} with $\psi_{\max}$ were statistically identical. The daily average diameter behaved like daily minimums with slightly lower degrees of explanation. On the other hand, F_{w} scaled by θ_{Amin}, θ_{Bmin} or $\psi_{\max}$ could explain the amplitudes best. All in all, when scaled, the daily maximum, minimum and average diameters seemed to vary closer with variables describing the driving force for transpiration and the amplitudes with the actual water vapor flux.

The daily maximum diameters were less well explained by all the environmental factors than the daily minimum or average diameters or the amplitudes. Rainfall events were related to the daily maximums so that after a rainy day, the maximum increased, but there was no correlation with the amount of rainfall (data not shown). However, periodically also the daily maximum diameter followed changes in the soil water content fairly thoroughly (Fig. 6) although the changes in the soil water content were still more prominent in the daily minimum diameters.

Discussion

Plant water use and response to varying soil water availability may have their basis in alternating the hydraulic conductance from soil to canopy (Sperry *et al.* 2002). The main changes in hydraulic conductivity from the soil through the plant to the atmosphere result from (I) changes in conductivity between bulk soil and the root as a function of soil water content (Newman 1969), (II) stomatal regulation of water loss (i.e. change in the force inducing tension), and (III) embolisation of conduits in the sap wood (Tyree and Sperry 1989). Diurnal xylem diameter variations are a measure of the tension in the sap experienced by the plant that is the balance between the two first types of changes and causes the third. The tension may also have a feedback connection to the second type and thus regulate it (Sperry *et al.* 2002).

Our long data series of daily xylem diameter variations showed that ψ had a closer relationship with the diameter values than θ. This emphasizes that the amount of soil water available and experienced by a plant does not coincide directly with the volumetric water content of the soil. Also the fact that the daily maximum diameters, although varying with rainfall events, did not depend on the amount of rainfall can be understood in the light of that.

The daily maximum diameter is a measure of to what extent the plant is able to refill the stem during stomatal closure (i.e. how close to equilibrium with soil water potential the plant can get). Variations in the maximum diameter are thus linked with the soil water potential that the roots are experiencing. In a perfect case they should follow the soil conditions but if excessive embolism did take place, then this connection would be lost. Although in late summer 2002 the soil was dryer than in any other summer analyzed here, the maximum diameters followed the pattern in the soil water content (Figs. 2 and 4) and the bulk canopy conductance did not change dramatically (Fig. 3; *see* also Goldstein *et al.* 2000). We can thus conclude that we did not see very severe loss of hydraulic conductivity of the sapwood. The measurements of ultra-acoustic emissions (UAE) from the same trees performed during the same period indicated that at maximum about 2% of the tracheids embolised daily but most of the time the value was much lower (Hölttä *et al.* 2005).

Our results also show that the daily maximum diameters correlated better with variables related to the soil water availability than those related to transpiration. During the year 1999 there was an obvious linkage between the two variables (Fig. 6) similar to that observed by Offenthaler *et al.* (2001). This further stresses the refilling aspect of the daily maximums. The pattern of UAEs also suggested that the previously embolised tracheids refilled during periods of lower water demand and better supply associated with rainfall events (Hölttä *et al.* 2005). The lower correlation of the daily maximums than daily minimums with any environmental variables indicates that the refilling capacity is, to some extent, independent of small variations in water availability as long as there is water available.

In the absence of severe embolism, the daily minimum diameter shows the highest tension obtained. Their higher correlation with soil water availability than with transpiration-related variables supports the observations of Tyree and Sperry (1988), that plants uptake carbon (and as a result transpire) as much as they can as long as there is no danger of severe damage to the functioning of the plant. Thus, water availability can be seen as a factor regulating the highest tensions obtained as suggested by Sperry *et al.* (2002). The daily average diameter followed the daily minimums closer than the daily maximums because the minimums varied more than the maximums.

In most of the years the early May values did not give the annual maximum diameters. It has frequently been suggested that low water availability in the soil could limit the spring recovery of evergreens in the north (Jarvis and Linder 2000). Recently Suni *et al.* (2003) and S. Sevanto *et al.* (unpubl. data) have shown photosynthetic production and water uptake from the soil during winter in favorable weather conditions even if the soil was frozen. It also seems that a considerable proportion of the soil water remains unfrozen in the soil profile all through the winter (Suni *et al.* 2003, S. Sevanto *et al.* unpubl. data). However, partially frozen water or low soil temperatures that lead to high viscosity of soil water would naturally decrease the water availability to the shoots, which would explain why the maximum diameters were not observed in early May. The difficulty of water uptake was not very likely to decrease the productivity in early May as considerably lower diameter values were observed later on in the summer during each of the observation years.

Daily amplitudes as a measure of the difference of the highest daily tension and the refilling ability should be highest when soil water is readily available (low tension in the stem at night and no need for stomatal regulation) and transpirational demand is high (high VPD and PPFD). Our results suggest again that the soil water content was more important in determining amplitude values than the transpirational demand (Table 1). The decrease of amplitudes with the increasing soil water contents is due to the tendency of low transpirational demand on periods of the high soil water content (i.e. soil water content is negatively correlated with maximum VPD). The non-linear relationship of amplitudes with PPFD can result from several factors. A negative correlation of the soil water content and maximum PPFD at high (> 500 μmol m^{-2} s^{-1}, *see* Fig. 5) PPFD values (i.e. soil dries in sunshine) and stomatal regulation would give a similar response.

The improvement in explicability by scaling transpiration-related variables with soil water content-related variables emphasizes the connection of diurnal diameter variations and water tension. It also shows that both factors affecting the outflow and inflow have to be considered in order to explain the water status of the stems (*see* also Perämäki *et al*. 2001). Scaling with the water content of humus layer always gave lower coefficients than scaling with either θ_A or θ_B indicating a closer relationship of stem water balance with the water content of deeper soil layers. This is contradictory to the distribution of roots at our site. Ilvesniemi and Liu (2001) reported that most root surface area was found in the humus layer. According to these results, it seems that even if there were many roots in the humus layer, the daily stem water content does not follow the rapid changes in θ_h. This may be due to either a very shallow ψ-θ curve in the humus layer or the inability of the roots to utilize all the water available during and after rainfall, but also the higher hydraulic permeability of larger roots that are typically deeper in the soil (e.g. Kramer and Bullock 1966). Evolutionarily, it is beneficial for trees to rely more on water reserves in deeper soil, since the conditions there are more stable.

The fact that all the scaling factors obtained from volumetric soil water contents gave better correlations when the transpiration-related variable was enhanced with low soil water contents (scaled by θ_{min}), but ψ gave better correlations when scaled with the opposite effect (ψ_{max}) reflects both the inability of variation in θ to describe what plants experience and the relationship between θ and ψ (*see* Fig. 2). All in all, the variation in stem diameter was not extremely well explained by any of the factors studied here. That points out the connection of diurnal diameter variation with physiological and structural aspects of trees (*see* Perämäki *et al*. 2005).

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Received 11 April 2005, accepted 1 August 2005