Trees (2000) 15:50–57
DOI 10.1007/s004680000072

ORIGINAL ARTICLE

Roman Zweifel · Hans Item · Rudolf Häsler

Stem radius changes and their relation to stored water in stems of young Norway spruce trees

Received: 26 July 1999 / Accepted: 20 August 2000 / Published online: 12 October 2000

Abstract Changes in the stem radius of young Norway spruce [*Picea abies* (L.) Karst.] were related to changes in stem water content in order to investigate the relationship between diurnal stem size fluctuations and internally stored water. Experiments were performed on living trees and on cut stem segments. The defoliated stem segments were dried under room conditions and weight (W), volume (V), and xylem water potential (Ψ_s) were continuously monitored for 95 h. Additionally, photos of cross-sections of fresh and air-dried stem segments were taken. For stem segments we found that the change in V was linearly correlated to the change in W as long as Ψ_s was >–2.3±0.3 MPa (phase transition point). Stem contraction occurred almost solely in the elastic tissues of the bark (cambium, phloem, and parenchyma), and the stem radius changes were closely coupled to bark water content. For living trees, it is therefore possible to estimate the daily contribution of "bark water" to transpiration from knowledge of the stem size and continuous measurements of the stem radius fluctuations. When Ψ_s reaches the phase-transition point, water is also withdrawn from the inelastic tissue of the stem (xylem), which – in the experiment with stem segments – was indicated by an increasing ratio between ΔV and ΔW. We assume that for Ψ_s below the transition point, air is sucked into the tracheids (cavitation) and water is also withdrawn from the xylem. Due to the fact that in living *P. abies* Ψ_s rarely falls below –2.3±0.3 MPa and the xylem size is almost unaffected by radius fluctuations, dendrometers are useful instruments with which to derive the diurnal changes in the bark water contents of Norway spruce trees.

Keywords Water relations · Bark water storage · Point dendrometer · Cavitation · *Picea abies*

R. Zweifel · H. Item · R. Häsler (✉)
Swiss Federal Institute WSL, Zürcherstrasse 111,
8903 Birmensdorf, Switzerland
e-mail: haesler@wsl.ch

Introduction

A dendrometer is a non-destructive instrument used for the continuous measurement of stem radius fluctuations. To understand how these diurnal fluctuations of stem size are related to dynamics of water storage, it is essential to know where the contractions/expansions occur and how these fluctuations affect the tissue water contents of bark and wood. To understand tree water relations, it is also important to investigate where water is stored in a stem and what proportions of the stored water are available for transpiration within the typical range of xylem water potentials (Ψ_s).

About three to four decades ago, Fritts (1961), Kozlowski and Winget (1964), and Impens and Schalck (1965) reported that dimensional changes in the stem are due to both growth and changes in hydration. Since these studies, dendrometer measurements have been associated with the water relations of trees in many ways. Hinckley and Bruckerhoff (1975) showed a significant correlation between pre-dawn Ψ_s and stem circumference once growth ceased in *Quercus alba*. In *Picea abies* [(L.) Karst.], Herzog et al. (1994, 1995) have demonstrated correlations between the stem radius and either transpiration or xylem sap flow. Panterne et al. (1998) presented a model that relates the water potentials within a stem (xylem and bark) with the corresponding stem radius changes. Zimmermann (1983) combined different insights and propounded a theory which couples the release of stored water from different locations to a corresponding range of Ψ_s. He distinguished three different locations of water storage in trees: (1) the xylem of the sapwood, (2) capillary storage in cell walls or within inactive vessels of the xylem, and (3) storage within living cells.

1. The water in the xylem of the sapwood is mainly in the form of water columns and the water of this tissue is only available when the negative Ψ_s exceeds the strength of cohesion among the water molecules. Under these conditions, cavitation occurs, and air bubbles are sucked into water-filled lumina (Tyree and

Sperry 1989). Lu et al. (1996) reported that embolisms started to develop in branches of *P. abies* when the water potential fell below a threshold of ca. –2.5 MPa (phase-transition point).

2. Capillary water is stored in the lumina of inactive xylem elements and in the intercellular spaces of the inelastic tissues of the xylem. Capillary water is released at relatively high Ψ_s, and the maximum release occurs at about –0.2 MPa (Tyree and Yang 1990). For Ψ_s <–0.5 MPa, the locations containing capillary water are almost entirely empty (Siau 1984). The depletion of capillary water in tissues is reversible and depends only on the actual Ψ_s.
3. The water stored in living cells can be withdrawn within the entire natural range of Ψ_s in the stem. Living cells in the stem are mainly located in the bark (phloem, cambium and parenchyma) and in wood rays. The depletion of water in living cells is reversible as long as the cell water content or water potentials do not decrease below a cell-damaging level.

However, Zimmermann's (1983) theory does not thoroughly explain the relationship between stem radius changes and tree water relations, and there is also the controversy concerning the origin of stem fluctuations. Irvine and Grace (1997) recently reported changes in the diameter of the sapwood due to the tension within the xylem, whereas Dobbs and Scott (1971), Molz and Klepper (1973), Siau (1984), and Brough et al. (1986) showed that stem radius fluctuations are mainly determined by water content changes within the bark. The fluctuations of xylem size in their study accounted for only about 10% of the entire stem radius changes.

In our experiments we tested these ideas by using continuous measurements of weight (W), volume (V), and Ψ_s, of air-drying stem segments of young *P. abies*. Additionally, photos of cross-sections of fresh and dry stem segments were taken to illustrate the locations of the shrinkage.

Materials and methods

Trees: potted Norway spruce

Six 4-to-6-year-old Norway spruce trees (*P. abies* L. Karst) were grown outdoors in a nursery in circular pots [volume, 13 l; substrate, 30% peat (by weight), 70% Toresa; fertilizer, 3 g Osmocote Plus l^{-1}, 3 g hornmeal l^{-1}, pH ca. 4.5]. Tree ages and their most important dimensions are listed in Table 1.

Experiments

The young trees were brought into the laboratory in front of an east-facing window 2 days before starting the experiments. After the acclimatization phase, the stem radii of the trees A, B, and C were continuously measured with point dendrometers over 8 weeks. The dendrometers, consisting of a precision displacement transducer (TRANS-TEK, USA) and a body of stainless steel were fixed to the pot at opposite sides. The sensing head was glued with tar to the smoothed bark surface at about 0.2 m above the soil. To avoid temperature effects, pots and dendrometers were shielded from direct sunlight by aluminum foil. The readings of the dendrometers (resolution 1.5 μm) were measured at 5-s intervals, averaged every 10 min and recorded by a data logger (CR7, Campbell, USA). During this period, the soil matric water potential in the pots was always kept at >–10 kPa. It was measured with syringe-type tensiometers (Ballmoos, Switzerland) (Marthaler et al. 1983). The relative humidity in the room varied within a range of 30–40%, and the temperature was between 20°C and 23°C.

After 8 weeks, the stems of all six experimental trees were cut into segments at dawn when Ψ_s was highest. The cuts were made just above and below the whorls. Thus, the length of the (branchless) segments varied between 0.1 m and 0.25 m depending on the annual length increments of the stem. Needles were removed and the initial values of diameter ($2R$) (slide caliper) and W (H33 AR, Mettler, Switzerland) were measured on each of the 33 stem segments. Assuming a homogenous Ψ_s along the stem, the starting values of Ψ_s were measured on the top segments of the trees immediately after cutting (pressure bomb; Walz, Germany). These top pieces were the only segments which were cut at one side only. Therefore they were useful for the application of Scholander's approach for water potential measurement (Scholander et al. 1965). Photos of the cross-sections of three stem segments were taken with a camera on a microscope and under direct light (enlarged 13 times).

The stem segments were then air-dried for 95 h in the same room. Simultaneously, we measured W of 14 segments, the radii of 13 segments and Ψ_s of 6 segments of the treetops (increment of the current year). For the radius measurements, the segments were fixed at one end in a vice. The dendrometer body was clamped to the vice and the sensing head was glued to the smoothed bark surface of the stem segment, in the same way as described for the living trees. During the first 3 h, Ψ_s was measured at 10- to 20-min intervals. The recording frequency was then reduced to 3–5 measurements day^{-1}. W and radius were automatically recorded at a 10-min interval. Ψ_s was recorded manually.

After the air-drying period of 95 h, the final $2R$ and W were measured on each of the 33 stem segments. Photos were taken of the same segments as at the beginning of the experiment.

Estimation of V

The changes in stem radius at the stem base (ΔR) were used to calculate the changes in stem volume (ΔV) assuming that ΔR remained constant over the entire stem length. To estimate the radius from tree height we used a modified formula from Roiko-Jokela (1976):

$$R(h) = \frac{R_0 \ln(h_{Top} - h + 1)}{\ln(h_{Top} + 1)} \quad (1)$$

Table 1 Dimensions of the stems of the potted Norway spruce trees (*Picea abies*) investigated

	Tree A	Tree B	Tree C	Tree D	Tree E	Tree F
Age (years)	6	6	6	6	4	4
Height (h_{Top}) (m)	1.18	1.12	1.16	1.14	0.61	1.10
Radius at base (R_0) (mm)	14.5	14	13.5	14.5	11.5	16.3
Stem volume (V) ($10^{-6}m^3$)	311	274	265	300	95	364

where $R(h)$ is the radius at height h (metres), R_0 is the radius at the stem base and h_{Top} is the tree height (Fig. 1). The coefficient of determination was >0.98 for each of the experimental trees. V can be written as the integral:

$$V = \int_0^{h_{Top}} R^2(h)\pi\, dh$$

$$V = \frac{R_0^2\pi}{\ln^2(h_{Top}+1)}\left\{\left[(h_{Top}+1)\left(\ln^2(h_{Top}+1) - 2\ln(h_{Top}+1)+2\right)\right]-2\right\} \quad (2)$$

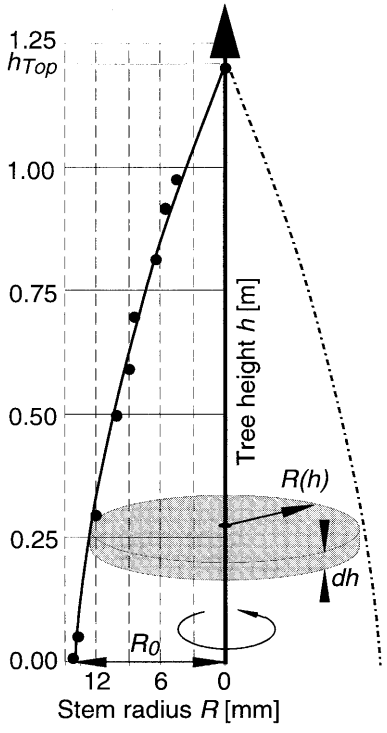

Fig. 1 The stem volume (V) as estimated with an integral of the logarithmic function of the radius [$R(h)$] over tree height; • indicate stem radius measurements on a potted *Picea abies*. R_0 Radius at the stem base, h_{Top} tree height, dh infinitesimal height of a stem disc for calculating V

ΔV can be derived from Eq. 2 as:

$$\Delta V = \int_0^{h_{Top}} [R(h) - \Delta R^2]\pi\, dh - \int_0^{h_{Top}} [R(h)]^2\, \pi\, dh$$

$$\Delta V = \frac{R_0 2\pi\Delta R}{\ln(h_{Top}+1)}\left[(h_{Top}+1)\ln(h_{Top}+1) - h_{Top}\right] + R^2\pi h_{Top} \quad (3)$$

Results

Air-drying stem segments

Figure 2 shows the normalized data of weight lost [$\Delta W(t)$], volume change [$\Delta V(t)$] and xylem water potential [$\Psi_s(t)$], measured on air-drying stem segments over 95 h. The stem segments proportionally lost V and W during the first 8 h, then the stem segment shrinkage became smaller and ΔV was no longer proportional to ΔW. Ψ_s decreased sharply during the first 5–8 h and then levelled off (Fig. 2b). Although the samples were cut at dawn and Ψ_s was measured immediately after cutting, Ψ_s was not greater than –0.2±0.1 MPa. Measured values for the changes (dy) of V or W with time (t) can be approximated by the function:

$$\frac{dy}{dt} = \alpha\left(\arctan\left(\frac{\beta}{t}\right) - \operatorname{arccot}(0)\right) \quad (4)$$

where α and β are experimentally determined parameters for V and W, respectively, i.e. for V, α=2.12, β=25.95; for W, α=11.50, β=142.3.

The sigmoid course of the $\Psi_s(t)$ measurements can be approximated by the equation:

$$\psi_s(t) = -\exp\left(\frac{-a + \arctan(t)}{t}\right)b - 0.2 \quad (5)$$

where a and b are experimentally determined parameters averaged over the six trees (a=3.57, b=3.15).

Photos of the cross-section of a stem segment in the fresh and the dry state (Fig. 3) show that the stem radius

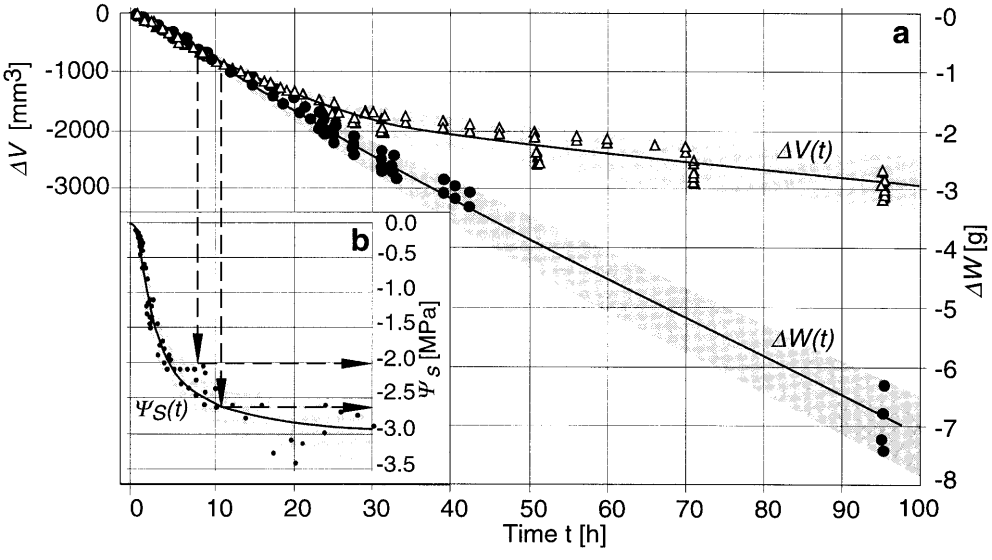

Fig. 2 **a** The loss of volume (ΔV) and weight (ΔW), and **b** the decrease in the xylem water potential (Ψ_s) in air-drying stem segments during 95 h. The two arrows show the period during which $\Delta V(t)$ begins to diverge from $\Delta G(t)$ to the corresponding Ψ_s. The *grey areas* mark the scatter of the measurements

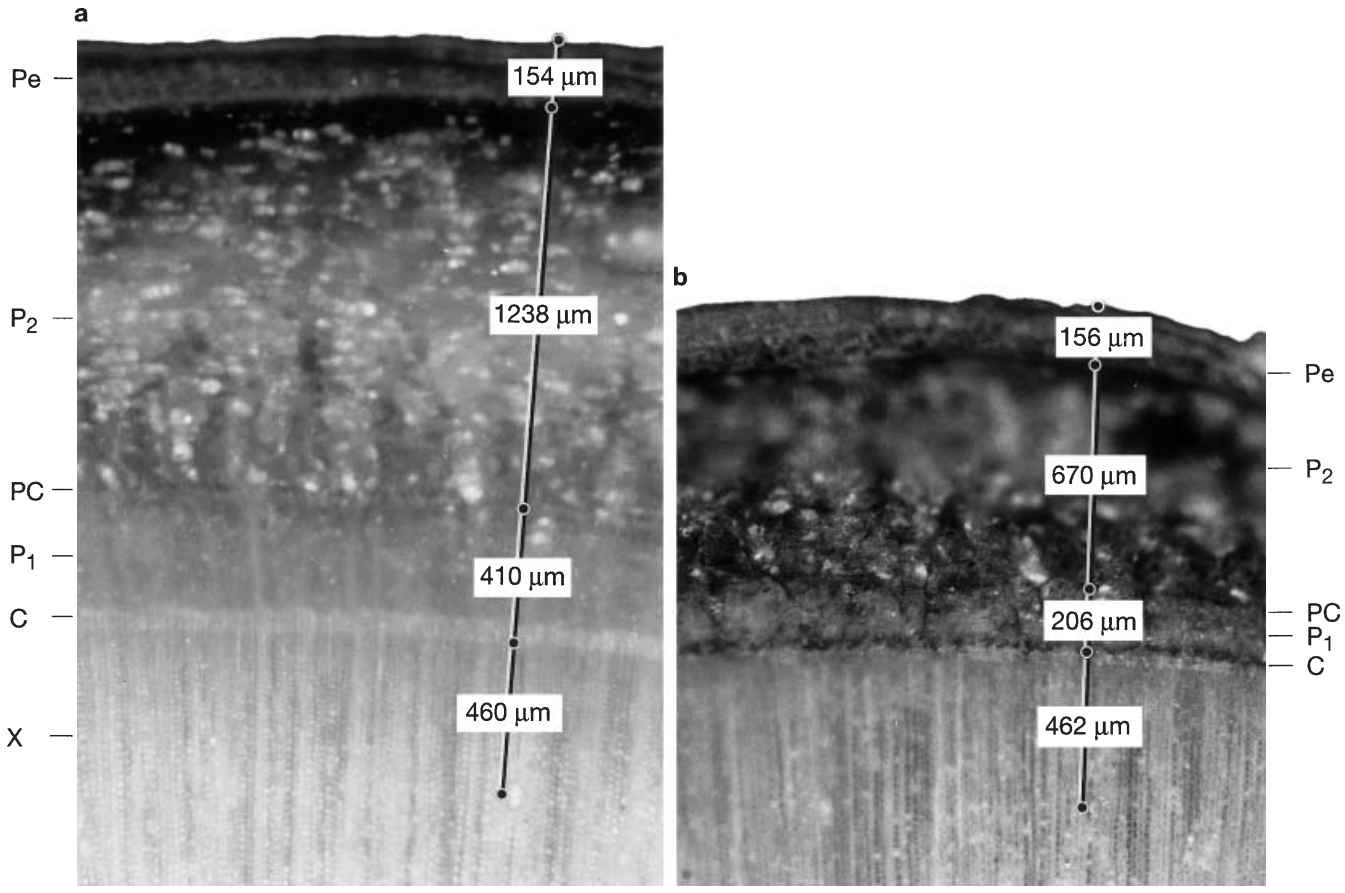

Fig. 3 Photos of a cross-section of the same stem segment of *P. abies* (**a** fresh, **b** air-dried). *X* Xylem, *C* cambium, P_1 phloem of the current year, *PC* parenchyma cells of the current year, P_2 phloem and parenchyma of preceding years, *Pe* periderm

contraction occurred in the elastic living tissues of the bark (cambium, phloem, and parenchyma). The bark tissues shrank to about 50% of their original size, whereas the xylem and the periderm underwent no contraction. Re-wetting of the dry pieces of wood re-hydrated the bark, and the phloem almost regained its original size.

Figure 3 corresponds to the dehydration data. Even when water was withdrawn from the xylem, this inelastic tissue did not change its size. The ratio $\Delta W/\Delta V$ was almost constant at 1.02±0.14 mg mm^{-3} as long as Ψ_s did not reach the phase-transition point at –2.3±0.3 MPa (Fig. 4). For Ψ_s below the phase-transition point, the ratio $\Delta W/\Delta V$ continuously increased, and at the end of the drying experiment (95 h), the ratio reached a value of 2.6±0.5 mg mm^{-3}. The air-drying period can be roughly divided into two phases: a first phase, during which the amount of water lost from the stem segments is linearly correlated to stem radius, and a second phase, where the relation is not linear, which means that the evaporated water will not be expressed as a volume change. The transition between the two phases can be assigned to a range of Ψ_s between –2.0 and –2.6 MPa (Fig. 4).

Water storage dynamics in living trees

Assuming Ψ_s to be above the phase-transition point, diurnal changes in stem water content (WC_{stem}) can be calculated from stem size and continuous measurements of stem radius fluctuations of living trees. The diurnal course of the stem radius measured on one of the experimental trees is shown in Fig. 5a. There was a considerable range in the fluctuations of daily stem radius (Fig. 5b). In our study, these fluctuations were mainly determined by sunlight, which increased the transpiration rate. On sunny days, stem shrinkage was greater than on cloudy days. During the 8 weeks of the experiment, the maximum difference between the *diurnal* maximum and minimum values of the stem radius (ΔR_D) was 70 μm, 74 μm, and 62 μm for trees A, B, and C, respectively. The substitution of ΔR in Eq. 3 by a measured value yields ΔV, which corresponds to the quantity of water that is withdrawn from the elastic storage tissue in the bark. Thus, ΔR_D indicates the maximum difference between the diurnal maximum and minimum values of the stem volume (ΔV_{max}). The largest amount of ΔV_{max} within the 8 weeks of the experiment approximates to the 1-day storage capacity of a tree stem ($ODSC_{Bark}$), the maximum amount of water that can be contributed to transpiration in a single day. The values listed in Table 2 show that $ODSC_{Bark}$ amounts to <2% of the total WC_{stem}.

V of the stem segments is mainly determined by the amount of available water in the bark (aw_{Bark}), which de-

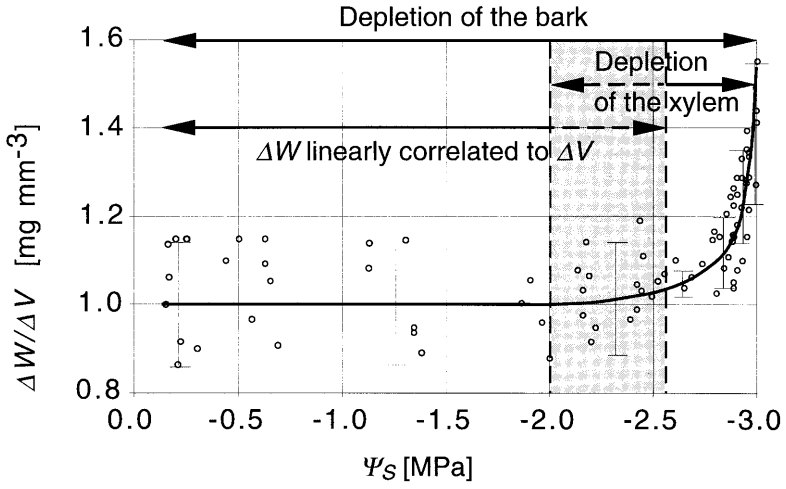

Fig. 4 Relationship between ΔW and ΔV of air-drying stem segments with a decreasing Ψ_s. The *grey area* indicates the range of the phase transition. For abbreviations, see Fig. 2

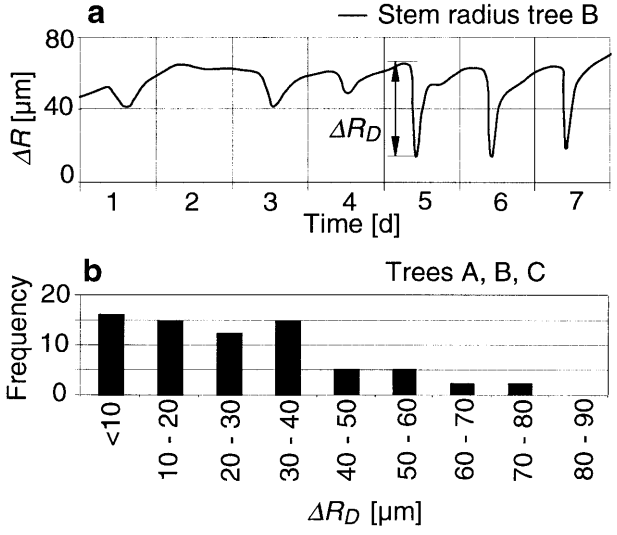

Fig. 5a, b Diurnal stem radius changes of potted *P. abies*. **a** Stem radius changes (ΔR) recorded at the stem base of tree B by a point dendrometer. Days 1–4 were cloudy, the following 3 days were sunny. **b** The frequency distribution of stem shrinkage within 1 day (ΔR_D) (trees A–C)

pends on the actual Ψ_s. A desorption curve for defoliated stem segments [$\Psi_s(aw_{Bark})$] is depicted in Fig. 6. The equation for the curve is:

$$\psi_s(aw_{Bark}) = \frac{-\psi_{s\,min}}{\exp\left(\frac{-k_1 + aw_{Bark}}{k_2}\right) + 1} \quad (6)$$

where $\Psi_{s\,min}$ is the minimum water potential of the stem, k_1 is the value of the water storage with the steepest slope of $\Psi_s(aw_{Bark})$, and k_2 determines the slope of $\Psi_s(aw_{Bark})$. The parameters in Eq. 6 were estimated for water potential measurements above –2.0 MPa by non-linear regression with least squares ($\Psi_{s\,min}$=–2.6 MPa, k_1=2.79, k_2=0.078). For the corresponding measurements on twigs (with needles) we used the same approximative function ($\Psi_{s\,min}$=–2.8 MPa, k_1=15.5, k_2=2.2) (data not shown).

Table 2 The maximum observed difference in stem radius within 24 h (ΔR_D) in three experimental trees and the corresponding 1-day water storage capacity ($ODSC_{Bark}$). WC_{Stem} Total water content per stem

	Tree A	Tree B	Tree C
ΔR_D (μm)[a]	70	74	62
$ODSC_{Bark}$ (g)	4.26	4.12	3.45
WC_{Stem} (g)	245	205	195
$ODSC_{Bark}\,WC_{Stem}^{-1}$ (% vol.)	1.7	2.0	1.8

[a] Recorded at the stem base

Discussion

Relationship between stem size fluctuations and water storage

In young *P. abies*, stem size fluctuations are proportionally related to the bark water content as long as Ψ_s does not sink below the phase-transition point at –2.3± 0.3 MPa. Above this transition point, water is mainly withdrawn from living cells in the bark and other tissues are not depleted of water. This was also suggested by Holbrook (1995) from studies on living trees. The change of cell water content is solely responsible for the volume change of a stem, and radius fluctuation is mostly restricted to extensible tissue outside of the cambium. This finding corresponds with the results of Dobbs and Scott (1971), Molz and Klepper (1973), Siau (1984), and Brough et al. (1986), but it is in contrast to that of Irvine and Grace (1997). They reported changes in the diameter of the sapwood due to the tension within the xylem of *Pinus sylvestris*. Such a contraction of the sapwood cannot be completely excluded in *P. abies*, but recently reported investigations on mature *P. abies*, in which point dendrometers were separately mounted onto bark and xylem, showed that the fluctuation of the xylem was <10% of the entire radius fluctuation (Zweifel and Häsler 2000). Nevertheless, we agree with Holbrook (1995), Irvine and Grace (1997), and Panterne et al.

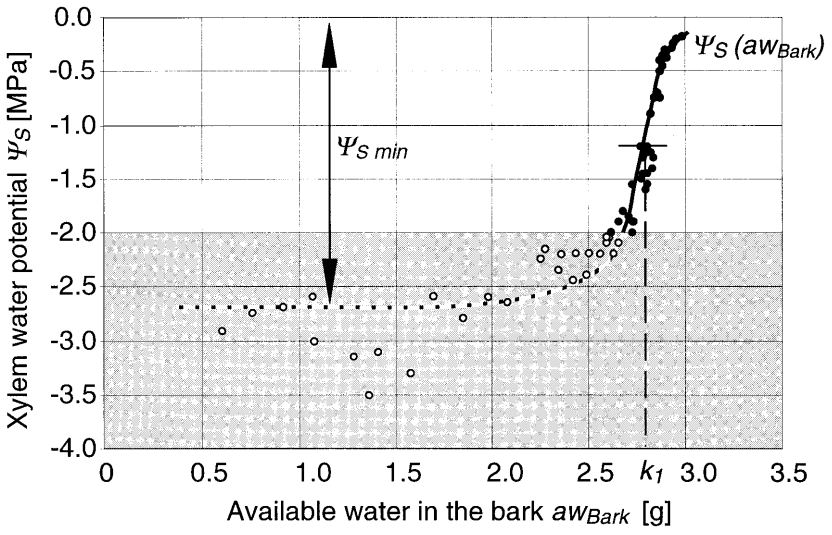

Fig. 6 Water desorption curve for stems of *P. abies*. The function $\Psi_s(aw_{Bark})$ is fitted to measurements within the natural range of Ψ_s in living trees ($\Psi_s > -2.0$ MPa). The resulting $\Psi_{s\ min}$ therefore does not perfectly represent the measurements. k_1 marks the turning point of $\Psi_s(aw_{Bark})$

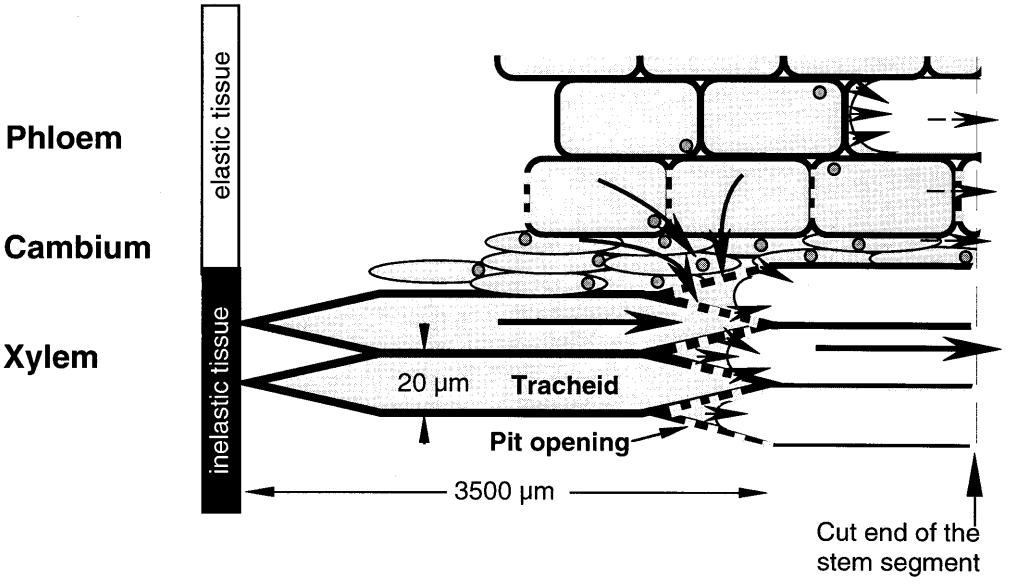

Fig. 7 Model for the dehydration of a stem segment. Water flows from the bark into the xylem and evaporates through the cut ends

(1998) that changes in diameter are valuable as an index of Ψ_s.

A proposed mechanism of water release from drying stem segments

With the cutting of the trees into stem segments, water began to evaporate and the segments linearly lost V and W. In contrast to similar investigations by Zimmermann (1983) and Tyree and Yang (1990) we observed no release of capillary stored water from inelastic tissues at Ψ_s close to zero. At least at the beginning of the air-drying experiment, we expected to measure the release of capillary water due to the release of water from water-filled tracheids and parenchyma cells at the cut ends. Capillary water evaporates rapidly from the rigid vessels and therefore, under these conditions, the $\Delta G/\Delta V$ ratio should increase. However, this was not the case here. We assume that at the time of cutting the stem, the water in the cut tracheids was immediately sucked back into intact tissues of the stem due to the slightly negative Ψ_s of approximately –0.2 MPa.

We suggest that most of the water was evaporating through the cross-sectioned areas of the defoliated stem segments (Fig. 7). During the first phase of the drying experiment, the water content in the wood remained the same, whereas the bark proportionally shrank with weight loss. It is concluded that the evaporated water from the xylem was simultaneously replaced by water withdrawn from the bark. Comstock (1970) and Spolek and Plumb (1981) showed how the structure of softwoods can support radial water flow along a gradient within the xylem of drying wood. Water from the phloem reaches the xylem in wood rays and also by crossing the cambium (symplastic and apoplastic) and entering the tracheids through the pits. The radial water flow through the xylem enables rapid transport of water from

the bark towards the centre of the stem and also to the cut ends. Due to this water transport from the bark into the xylem, the tracheids remained water-filled despite the lowered water content of the entire stem segment.

The water content of the wood decreased significantly when Ψ_s fell below the phase-transition point of –2.3±0.3 MPa. We suggest that in this second phase of the drying experiment, air is sucked into the tracheids and thus, the water columns cavitate. Lu et al. (1996) reported that the occurrence of cavitation is related to the tree specific water potential (for *P. abies,* –2.5 MPa). This value is close to the phase-transition point of –2.3±0.3 MPa which we measured, and this indicates the initial depletion of water in inelastic tissues of the stem. The process of depleting the sapwood in cut stem segments of water is obviously not exactly the same as the process of cavitation in living trees. However, both processes have in common that air must be sucked into the tracheids before water can be released (Lambers et al. 1998). The water potential that is necessary to suck air into a lumen of a tracheid corresponds to the force which exceeds the surface tension and adhesion of water in the largest pore of the cell wall (Sperry et al. 1987). According to the capillarity equation, the larger a pore radius is, the smaller the tension in the lumen has to be in order to suck air into a tracheid. The radius of open pits in softwood is between 0.01 and 0.2 μm; the radius of the pores within the microstructure of the torus of closed pits is between 0.002 and 0.1 μm (Siau 1984). For a Ψ_s of –2.5 MPa, we calculated a corresponding pore radius of 0.06 μm by the capillarity equation. This value seems plausible, as it is within the range for a potential pore radius of closed pits. We assume, therefore, that the dehydration of the xylem by cavitation in cut stems as well as in living trees depends on the maximum pore radius in the tracheids.

Water storage dynamics in living trees

Aware that an air-drying stem segment is just a model for the depletion of water stored in the stems of living trees, we suggest that stem radius changes in living trees are also caused by changes in bark water content (Holbrook 1995). It is assumed that the morphological properties, e.g. the dimensions of the pores, are not changed through the cutting of the stem and that the tissue structures are mainly responsible for the sequence of the depletion of the different water reserves. Lu et al. (1996) reported that Ψ_S in *P. abies* rarely reaches the phase-transition point where cavitation would occur and water could be withdrawn from inelastic tissues. Therefore, water contributed from internal storage locations to transpiration can be calculated from stem size and continuous measurements of stem radius fluctuations. For the experimental trees, the maximal amount of available water withdrawn from the bark per day was about 2% of the total WC_{stem}, which corresponds to about 2–15% of the amount of water transpired daily. The physiological implications of these relatively small amounts of internally stored water contributing to transpiration are discussed in detail by Zweifel (1999).

In conclusion, continuous stem radius fluctuations provide much information about tree water relations. The chain of causes and effects can be summarized as follows: starting with the dendrometer measurements, the stem radius changes are coupled to the bark water content, and the bark water content is determined by water potential gradients ($\Delta\Psi_s$) within the xylem. Finally, $\Delta\Psi_s$ is coupled to the course of transpiration as well as to the soil water potential. Thus, the diurnal course of the stem radius is a very sensitive sum of all these factors. Nevertheless, to understand the dynamics of stem radius fluctuations in order to interpret, for example, effects of drought stress or other environmental impacts, additional investigations are needed.

Acknowledgements We thank Prof. Dr F. H. Schweingruber for methodical suggestions and W. Schoch and D. Mathies for taking the photos. We are indebted to Prof. Dr H. Flühler for critical comments on the manuscript and to Prof. Dr J. Innes and Mrs M. J. Sieber for editing the English.

References

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

Comstock GL (1970) Directional permeability of softwoods. Wood Fiber 1:283–289

Dobbs RC, Scott DRM (1971) Distribution of diurnal fluctuations in stem circumference of Douglas fir. Can J For Res 1:80–83

Fritts DC (1961) An evaluation of three techniques for measuring radial tree growth. Bull Ecol Soc Am 42:54–55

Herzog KM, Thum R, Häsler R (1994) Diurnal variation in stem radii and transpiration flow at different crown levels of a Norway spruce (*Picea abies* (L.) Karst.). In: Pfadenhauer J (ed) Verhandlungen der Gesellschaft für Ökologie. Gesellschaft für Ökologie, Freising-Weihenstephan, pp 143–147

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

Holbrook NM (1995) Stem water storage. In: Gartner BL (ed) Plant stems: physiology and functional morphology. Academic Press, San Diego, Calif, pp 151–174

Impens II, Schalck JM (1965) A very sensitive electric dendrograph for recording radial changes of a tree. Ecology 46: 183–184

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

Kozlowski TT, Winget CH (1964) Diurnal and seasonal variation in radii of tree stems. Ecology 45:149–155

Lambers H, Chapin FS, Pons TL (1998) Plant physiological ecology. Springer, Berlin Heidelberg New York

Lu P, Biron P, Granier A, Cochard H (1996) Water relations of adult Norway spruce (*Picea abies* (L.) Karst.) under soil drought in the Vosges mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation. Ann Sci For 53:113–121

Marthaler HP, Vogelsanger W, Richard F, Wierga PJ (1983) A pressure transducer for field tensiometers. J Soil Sci Soc Am 47:624–627

Molz FJ, Klepper B (1973) On the mechanism of water-stress-induced stem deformation. Agron J 65:304–306
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
Roiko-Jokela P (1976) Die Schaftformfunktion der Fichte und die Bestimmung der Sortimentsanteile am stehenden Baum. Mitt Eidgenöss Anst Forstl Vers wes 52:1–84
Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. Science 184:339–346
Siau JF (1984) Transport processes in wood. Springer, Berlin Heidelberg New York
Sperry JS, Holbrook NM, Zimmermann MH, Tyree MT (1987) Spring filling of xylem vessels in wild grapevine. Plant Physiol 83:414–417
Spolek GA, Plumb OA (1981) Capillary pressure in softwoods. Wood Sci Technol 15:189–199
Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. Annu Rev Plant Physiol Mol Biol 40:19–38
Tyree MT, Yang S (1990) Water-storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms. Planta 182:420–426
Zimmermann MH (1983) Xylem structure and ascent of sap. Springer, Berlin Heidelberg New York
Zweifel R (1999) The rhythm of trees – water storage dynamics in subalpine Norway spruce. PhD thesis no. 13391. Swiss Federal Institute of Technology (ETH), Zürich
Zweifel R, Häsler R (2000) Frost-induced reversible shrinkage of bark of mature, subalpine conifers. Agric For Meteorol 102:213–222