ORIGINAL ARTICLE

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Diurnal changes in the radius of a subalpine Norway spruce stem: their relation to the sap flow and their use to estimate transpiration

Abstract Diurnal changes in the stem radius of a subalpine mature Norway spruce were measured simultaneously with the flow of sap in xylem. Matric potentials in the soil were > -35 kPa. The kinetics of the flow were closely related to the changes in the radius of the stem resulting from depletion of its extensible tissues. The radius of the stem oscillated daily and, fairly independently of this, fluctuated over several days. The daily shrinkage (ΔS_d) was correlated with the daily flow through its base (Q_d). When the crown transpired little and was nearly saturated during rainy days, ΔS_d tended to increase relative to Q_d. Using a linear relation, the estimates of flow by ΔS_d deviated less than $\pm 10\%$ from the values measured by heat balance, provided that the periods of calibration in their ratio of dry to rainy days were comparable to those estimated. If the two periods differed in this respect, the estimates of flow deviated up to 42%. A quadratic relation yielded estimates that depended less on weather. It reduced maximal deviations to $\pm 22\%$. Since ΔS_d additionally may represent the time pattern of the daily transpiration better than Q_d, analysing changes in the radius of stems may supplement or partly replace measurements of sap flow in stems.

Key words Stem radius variation · Xylem sap flow · Crown transpiration · *Picea abies*

Introduction

The balance of the water within plants is determined by the relative rates of water loss and uptake. Transpiring surfaces draw not only on the water being absorbed by the roots but temporarily also on that stored in tissue. This is important for plants to respond rapidly to changes in transpiratory demand (Kozlowski et al. 1991). Those parts of plants from

which the water is withdrawn (e.g. fruits, stems, leaves) then may fluctuate in size.

The water stored within the trunks of trees may contribute substantially to their transpiration (Lassoie 1973; Hinckley and Bruckerhoff 1975; Waring et al. 1979). It may be stored either within the rigid woody tissues of xylem or within the extensible tissues of living cells of xylem, cambium and phloem, including the cambial initials. If water is withdrawn from woody tissue, cavitation rather than shrinkage occurs because the tissue is inelastic (Jarvis 1975). Thus, the contribution such water makes to transpiration depends on the time required for the recovery from cavitation (Waring and Running 1978). Although little is known about repair mechanisms of embolisms in xylem of tall trees, their recovery probably takes longer than 1 day (Tyree and Sperry 1989; Waring and Running 1978). Changes in the water content of extensible tissues in stems, however, are readily reversible. Those causing fluctuations in diameter and circumference have been well documented, since techniques to record them continuously have long been known (e.g. Fritts 1961; Impens and Schalck 1965). However, since such measurements were usually aimed at studying the growth of trees, little attention was paid to the water. Thus, fluctuations in size due to water have so far been of interest mainly to assess bias caused in measurements of the growth (e.g. Worrall 1966; Holmes and Shim 1968; Vogel 1994).

Diurnal fluctuations in size of stems were found to be caused mainly by peripheral tissue. They seem to result mostly from exchange of water back and forth between xylem and phloem, driven by the changing water potential in xylem (Dobbs and Scott 1971; Molz and Klepper 1973; Jarvis 1975). The theory of such a radial movement of water was substantiated by diffusion models established by Molz et al. (1973) and Parlange et al. (1975).

Internal stores of plants can be regarded as separate sources of water linked in parallel with each other and with the soil (Jarvis 1975):

$$E = Q_{soil} + Q_{store_1} + Q_{store_2} + ... + Q_{store_n}$$

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The flow from a particular store is

$$Q_{store_i} = \frac{\Psi_{store_i} - \Psi_{xylem}}{R_{store_i}}, \quad (i = 1, 2, ..., n)$$

where E is the transpiration, Q_{soil} is the absorption of water from the soil, Q_{store_i} is the water flow out of the storing tissue i, Ψ_{store_i} and Ψ_{xylem} are the water potentials in the tissue i and in the xylem, and R_{store_i} is the resistance to the movement of water from the tissue i to the xylem. In addition to the resistance between stores and xylem, the storage capacity and the moisture characteristic of individual tissues determine the amount of water withdrawn from them. When there is a plentiful supply of water from soil then extensible storage tissue is likely to be depleted and recharged in a daily cycle. If it is not completely emptied and if the resistances R_{store_i} of the flows out of all stores — including the soil — remain proportional to each other, the daily amount of water withdrawn from such tissue can be expected to be closely related to that absorbed by the roots and also to that transpired.

We pursued this idea and explored the relationship between the flow of sap through a stem and the withdrawal of water — measured as fluctuation in size — from extensible storage tissue.

Materials and methods

The measurements were made on a mature Norway spruce [*Picea abies* (L.) Karst.], aged about 220 years, during the growing seasons of 1992 and 1993. The tree was 25 m tall and had a diameter at breast height of 0.36 m. It was growing in a subalpine larch-spruce forest (*Larici-Piceetum*) 1639 m above the sea level near Davos (Switzerland). The living crown extended from the top of the tree to 3.5 m above the ground and had an estimated total surface area of needles of 447 m^2 (Häsler et al. 1991). The soil had been classified as a ferric humic podsol.

Dendrography

Dendrographs were attached to the stem 1.9 m, 11.8 m, and 19 m above the ground. They consisted of precision displacement transducers (TRANS-TEK, Ellington, Conn., USA) on frames of aluminum, and they were clamped to the measured sections and anchored from both sides 50 mm deep into hydroinactive xylem. Fixing the sensor to a frame in this way had two advantages over anchoring it directly at the measured location. First, the stem remained intact where it was contacted by the sensor, and second, any size fluctuation of the stem inside the anchoring could be accounted for. On the other hand, the frame caused bias because of its thermal expansion. This, however, was estimated never to exceed 10% of the shrinkage measured, even on the days with largest variation in temperature. The section of the stem where the dendrograph was mounted was kept dry by a plastic cover. The bias due to the hygroscopic swelling and shrinking of the bark at its surface was minimized by placing the contact point 5 mm below the surface. We tested this arrangement by enclosing the measured section together with a wet sponge by plastic foil. The measurement showed negligible response to its exposure to the vapor. Also the measured daily oscillation remained unaffected. Anchoring the contact point below the bark's surface had the further advantage that no pressure had to be applied to ensure a permanent contact with the stem. A magnetic coupling connected the contact point with the pin of the transducer to prevent this from getting wedged in the guide fixture. The voltages of the sensors were recorded every 15 min as the averages of 30-sec

readings. The daily shrinkage of the stem (ΔS_d) was calculated as the difference in the radius between the maximum in the early morning and the minimum during the day. Correspondingly, the nightly swelling of the stem (ΔS_n) was described by the absolute difference between the daily minimum of the radius and the maximum on the next morning.

Sap flow measurements

The flow of sap in the xylem was assessed by the heat balance within the tissue of the stem (Čermák et al. 1973; Kučera et al. 1977; Čermák and Kučera 1981). A flow meter (Gröger S. E. P., Bayreuth, Germany) was installed below the living crown at 3.3 m above the ground. The results of the flow meter were initially inaccurate. They were adjusted by reference to the gauge SGB25 (Dynamax, Houston, Tex., USA) that measured the heat balance of entire stems (Herzog 1995). The daily flow of the sap (Q_d) was calculated for the time between 0 and 24 h.

Environmental measurements

Matric potentials in the soil were obtained from tensiometers arranged in two transects crossing the area of the roots. We placed 14 of them at each depth of 10, 35 and 80 cm. The six tensiometers 1.3 m south and 1.3 m north of the trunk, which represented all depths, were continuously recorded by automatic pressure transducers. The continuous measurement was intended to recognize the behavior of the matric potentials, whereas periodic manual readings of all tensiometers allowed estimates of the distribution of potentials within the root area. The weather was recorded on the top of a 35-m tower near the experimental tree.

Estimations of sap flow

The sap flow in xylem was estimated over different periods by daily shrinkage of the stem. The following linear (Eq. 1) and quadratic (Eq. 2) relations of regression were used:

$$Q_d = a \cdot \Delta S_d \tag{1}$$

$$Q_d = b \cdot (\Delta S_d)^2 \tag{2}$$

The parameters a and b were estimated by fitting the data of the individual calibration periods. The parameter a ranged between 0.37 and 0.62, and parameter b for the two calibrated periods was 0.0031 and 0.0029. The average r^2 of all fits made by Eq. 1 and Eq. 2 were 0.77 and 0.78, respectively.

Results

Figure 1 shows the diurnal course of the changing radius of the stem together with that of the sap flow through it. Both factors were closely related and reacted sensitively to the weather. The fast temporary decline in flow on August 3 was reflected in a pulse through the stem, which was measured with a delay of about 1.5 h. The daily shrinkage of the stem was closely coupled to the daily flow through it.

The hysteretic relation between the diurnal courses of the two factors is shown in Fig. 2. At the beginning (August 28) and in the middle (September 3 to 5) of the period it rained, and hardly any flow occurred within the stem. During these days the stem expanded progressively. On the dry periods in between it shrank. When the tree had replenished its stores (August 29 and September 6) the stem began to shrink before the flow started. At large daily flows

Fig. 1 Diurnal courses of the sap flow through the stem and the change in its radius measured at the base between 1 August and 15 August 1992. —— Radius of stem; —— sap flow through stem
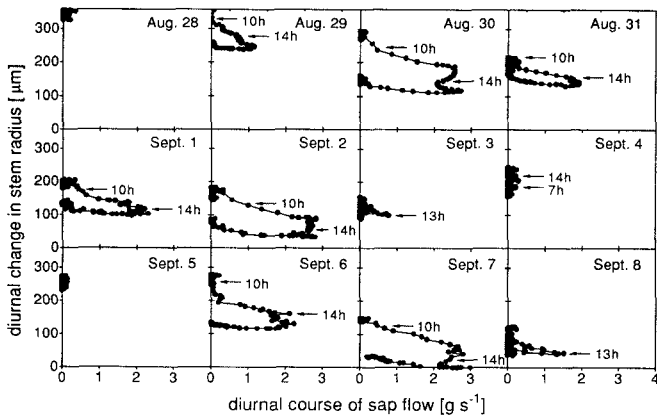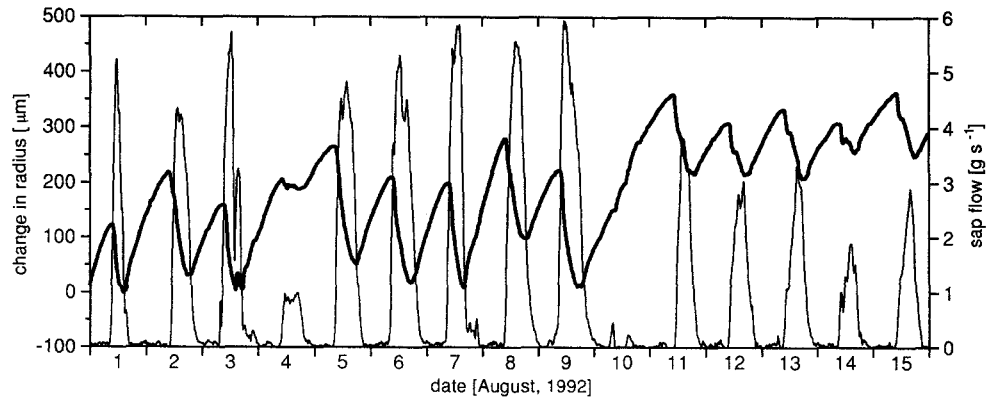

Fig. 2 Relation between diurnal courses of the radius and the flow of sap at the stem base during subsequent days with alternating wet and dry weather. Some points of time are indicated. Besides its daily oscillation the radius also fluctuated over several days. During the dry days it progressively decreased (e.g. 29 August to 2 September), during the wet days it increased (3 to 5 September 1993)

the stem could still shrink when the flow was already declining, until this fell below about 2 g s^{-1}. Once the flow was less than that value the stem started swelling again. On August 29 when the tree had become resaturated (cf. also Fig. 3) the stem shrank as much as on September 2, although the flow then reached only half the value of that day.

Some factors related to the water in the tree and its environment are shown in Fig. 3 for the main growing season of 1993. There was frequent rain; the matric potential in the soil decreased only slightly, and it reacted little to rain < 20 mm per day. The light rain was intercepted by the canopy and was not detected in the soil. On July 10 and between August 22 and 24 the daily rain exceeded 20 mm and reached the soil, which caused the matric potential to increase abruptly. The flow of the sap reacted sensitively even to light rain and was strongly affected by the interception of this by the crown. The availability of water in the soil, however, did not appear to affect it and probably never restricted the uptake of water by the roots. The fluctuations in the radius of the stem reflected the degree of the tree's saturation with water very sensitively. The daily shrinkage

Fig. 3 a–d Time series of different factors in water relations of the tree from July to September 1993. **a** the daily rain; **b** the daily flow of sap in xylem (Q$_d$) and the daily shrinkage (ΔS$_d$) and nightly swelling (ΔS$_n$) of the stem at 1.9 m above the ground; **c** the diurnal change in the radius of the stem at the heights of 1.9 m, 11.8 m, and 19 m; and **d** the matric potential in the soil at the depths of 10 cm, 35 cm, and 80 cm. Data of sap flow are missing between 25 and 28 August
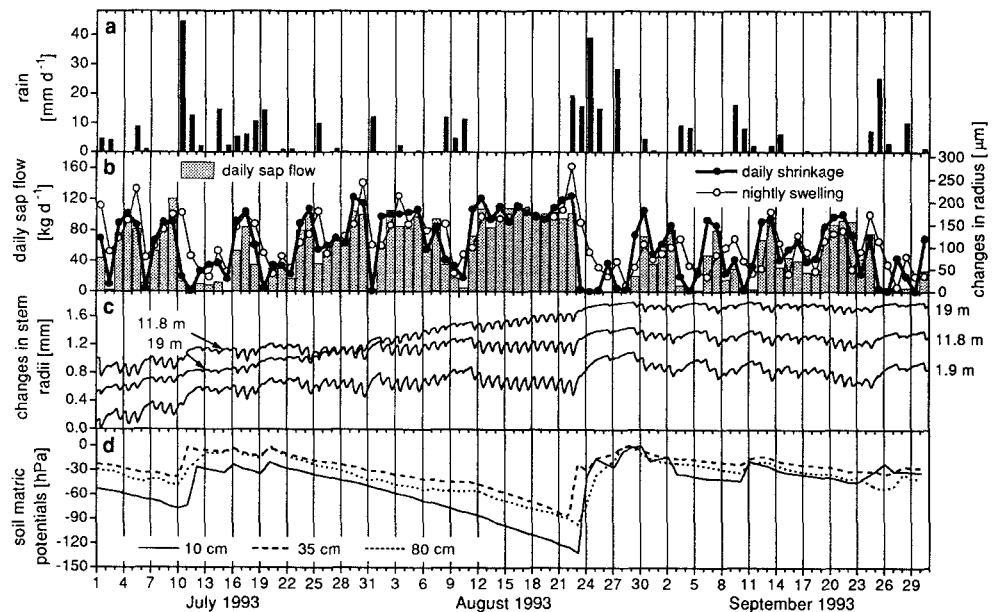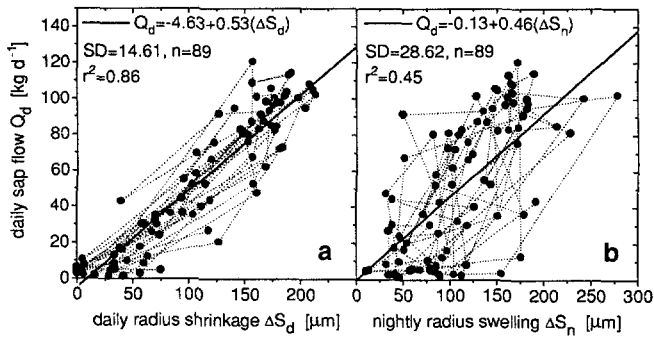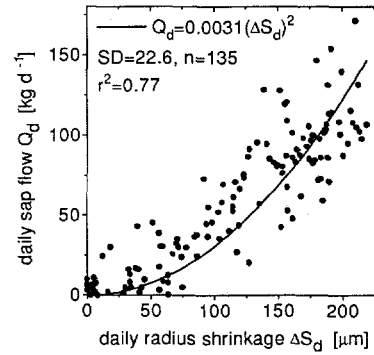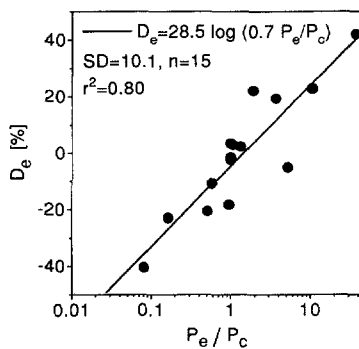
Fig. 4 Relations and linear regressions between the daily flow of sap (Q_d) and **a** the daily shrinkage of the stem (ΔS_d) and **b** the nightly swelling of the stem (ΔS_n), all measured at the base of stem. *Dotted lines* connect daily values and show the time behavior. The data represent the same period as shown in Fig. 3

Fig. 6 The quadratic relation (Eq. 2) for the estimation of the sap flow fitted to all data of measured daily flow (Q_d) and daily stem shrinkage (ΔS_d) at the base of stem

ΔS_d, measured at 1.9 m above the ground, developed a time pattern almost identical to that described by Q_d. The nightly swelling ΔS_n behaved similarly. Two conspicuous characteristics distinguished ΔS_d and ΔS_n in their time pattern from Q_d. The ΔS_d increased relative to Q_d when this was small during wet weather and on clear days succeeding such weather (Fig. 3: e.g. July 13 to 19, August 29 to 31, September 5 to 6, and 27 to 28). The ΔS_n, on the other hand, was disproportionately large when rainy days followed several dry days (e.g. July 5, 10, 25, and 30, August 3, 8, and 22, September 3, 9, and 24). The magnitude of ΔS_d, if measured at different positions along the stem, could differ considerably, but their time patterns were always nearly identical.

Figure 4 shows the relation of ΔS_d and ΔS_n to Q_d during the period described in Fig. 3. The ΔS_d was well correlated with Q_d (Fig. 4 a). The behavior in time – indicated by the dotted line – shows that ΔS_d and Q_d developed proportionally to each other except on some days with small Q_d. The ΔS_n, however, was only weakly correlated with Q_d (Fig. 4 b). This relation seems to be slightly hysteretic.

Fig. 5 The deviations (D_e) of the estimates by the linear relation (Eq. 1) from the measured flows in dependency on the weather during the periods of estimation and calibration (subscripts e and c, respectively). P describes the proportion of rainy to dry days during the periods. All days on which some rain occurred, independently of the quantity, were considered to be rainy

Table 1 lists the flows of sap estimated by ΔS_d and measured by heat balance for periods of different length and weather. If the linear relation (Eq. 1) is used to calibrate then the estimates deviate from measured values greatly depending on the weather during the calibrated period. Small deviations of -1.8% to $+3.3\%$ result if the calibration is made for the same period for which the estimates are made. If the calibration is made for only a few days within the estimated period or for days of the other year then the bigger the difference in weather between the periods of estimation and calibration the larger is the deviation. For August 1992 when the crown was predominantly dry, the flow is underestimated by 40.6% if the rainy period between 13 and 19 July 1993, is used for calibration. If the period of the calibration was drier than that of the estimation then the flows are overestimated. The dependency of the deviations on the proportions of wet and dry days during the periods of estimation and calibration is shown in Fig. 5. The length of the period used for the calibration is of little importance. The flow estimated from 1 July to 30 September 1993, using only 4 representative days to calibrate, deviates by $+2.2\%$ from the measured flow. Calibrating over 7 days between July 1 to 7 yields a deviation of $+2.8\%$. In both these cases, where short but well representative periods are used to calibrate, the deviation is smaller than that of $+3.3\%$ resulting from the calibration over the whole estimated period. The quadratic relation (Eq. 2) calibrated for contrasting weather yields estimates that are less affected by weather during the estimated period than those obtained from the linear relation. Estimates from it deviate within a range of $\pm 22\%$, even if the periods of estimation contrasted in weather. The quadratic relation fitted to all data is shown in Fig. 6.

Discussion

Measuring changes in the radius of stems has been criticized on the grounds that it would be significantly affected by the hygroscopic swelling and shrinking of stem surfaces

Table 1 The flow of sap through the stem as measured by heat balance and estimated by daily shrinkage of the stem (ΔS_d) using a linear and a quadratic relation. During all periods the matric potentials of water within the rooted soil area never decreased below -35 kPa. Classification of periods: "Wet" periods were dominated by rainy days. "Dry" periods were dominated by bright days. Periods of "dry-wet alternation" include about equal numbers of bright and rainy days. Precipitation for the periods of 1993 may be seen in Fig. 3

Periods				Sap flow during the periods		
Estimated periods	Calibrated periods	Days	Weather	Measured [kg]	Estimated [kg]	Deviation of estimates [%]
Calibrated by the linear relation (Eq. 1)						
1 July to 30 September 1993	Estimated period	89	dry-wet alternation	4659	4811	+3.3
	1 to 7 July 1993	7	dry-wet alternation		4791	+2.8
	30 July to 2 August 1993	4	dry-wet alternation		4760	+2.2
	13 to 19 July 1993	7	wet		3584	−23.1
	14 to 20 August 1993	7	dry		5714	+22.6
2 to 16 July 1992	Estimated period	15	wet	582	568	−2.5
	2 to 16 July 1993	15	dry-wet alternation		711	+22.0
	1 to 7 July 1993	7	dry-wet alternation		693	+19.1
	13 to 19 July 1993	7	wet		518	−11.0
	14 to 20 August 1993	7	dry		827	+42.0
1 to 31 August 1992	Estimated period	31	dry	2880	2828	−1.8
	1 to 31 August 1993	31	dry-wet alternation		2349	−18.4
	1 to 7 July 1993	7	dry-wet alternation		2287	−20.6
	13 to 19 July 1993	7	wet		1710	−40.6
	14 to 20 August 1993	7	dry		2727	−5.3
Calibrated by the quadratic relation (Eq. 2)						
	2 to 16 July 1992 and 14 to 20 August 1993	22	wet and dry			
1 July to 30 September 1993		89	dry-wet alternation	4659	4115	−11.7
2 to 16 July 1992		15	wet	582	563	−3.4
13 to 19 July 1993		7	wet	202	223	+10.1
1 to 31 August 1992		31	dry	2880	2273	−21.1
14 to 20 August 1993		7	dry	739	640	−13.4
	All periods	135	dry-wet alternation			
1 July to 30 September 1993		89	dry-wet alternation	4659	4303	−7.7
2 to 16 July 1992		15	wet	582	588	+1.0
13 to 19 July 1993		7	wet	202	233	+15.1
1 to 31 August 1992		31	dry	2880	2376	−17.5
14 to 20 August 1993		7	dry	739	669	−9.5

and therefore would not actually reflect the changing content of the water within them. Lövdahl and Odin (1992) found that the daily change in the diameter of stems of 3 to 6-year-old seedlings of Norway spruce remained unaffected, even if all needles had been removed. The authors concluded that the daily change in diameter was the hygroscopic response of the stems to air humidity. This was also to be expected in our measurements. With our arrangement, however, where the contact point of the dendrograph was set below the stem surface, bias due to the hygroexpansion of the bark could be avoided (cf. Materials and methods). Even if our measurements had included such bias they would probably have been less affected than those reported by Lövdahl and Odin (1992). Within the trunk of a tall tree there is more extensible tissue than within the stem of a young seedling. A larger change in the radius results, and bias due to the superficial hygroexpansion is a smaller proportion. Furthermore, the stem surface we examined was dead and fairly hydrophobic. It might have been less inclined to absorb vapor from the air than fresh surfaces of seedlings (cf. Odin and Openshaw 1971). The simultaneous recording of the radius of the stem and the flow through it reveals a close relationship between them (Fig. 1). The dendrograph was at the base of the tree

and was shaded by the canopy. Hence, it measured a stem section fairly decoupled from evaporative demand of the free atmosphere. Nevertheless, the radius there – similar to the flow – responded quickly to changes in weather. This adds to our evidence that the change in radius was driven endogeneously by the water potential in xylem and not by an exogeneous hygroexpansion.
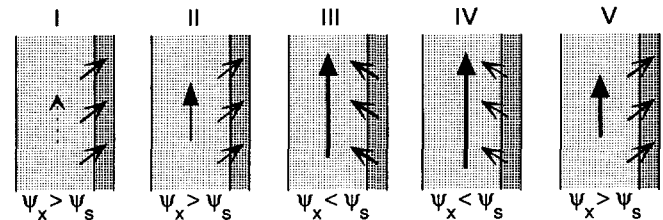
If we consider the plant as a hydraulic system, any change in pressure within the xylem will be transmitted to all parts of the plant. Small changes in the transpiration have an immediate effect on the water balance. A pressure wave starting from its site of initiation propagates throughout the plant. Because of the elasticity of the tissue, frictions in the path of the water, and the stores associated with the path, the pressure wave will diminish in amplitude and velocity as the distance from its source increases (Raschke 1970). The radius of the stem responded to fast changes in the flow through it with a delay of up to 2 h (e. g. Fig. 1: August 3). Milne et al. (1983) measured delays of up to 3 h until the basal radius of the stem of *Picea sitchensis* responded to a change in the transpiration and the water potential of the shoots. However, when our tree was saturated with water the stem shrank before the sap started flowing in its base (e. g. Fig. 2: August 29, September 6).
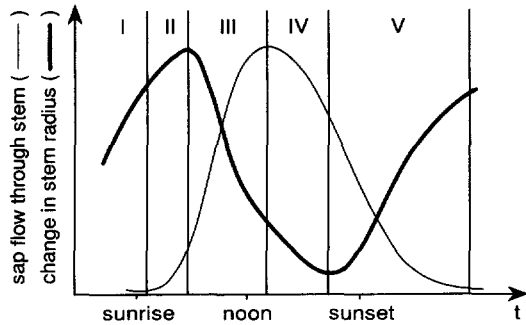
Fig. 7 Illustration of the main characteristics of diurnal flow of sap and change in radius of stem. Phase I is the nightly period of resaturation when there is no or little measurable flow. Phase II is the delay between the raise in flow and the start of decrease in radius. Phase III is the period of the fastest shrinking of stem until the flow reaches its maximum. Phase IV is the delay between largest flow and smallest radius at its reversal point. Phase V is the period in which the stem expands again while the flow gradually declines to the nightly level

Fig. 8 Schematic illustration of the diurnal flow of sap axially through the stem and the exchange of water back and forth between xylem (*light*) and storage tissue (*dark*) causing size fluctuation. The situations correspond to the five consecutive phases in Fig. 7. At the bottom of each, the gradient in water potential between xylem (ψ_x) and store (ψ_s), which determines the direction of the exchange, is indicated. The thickness of *arrows* indicates relative intensities of the flows during the day

This indicates that the sequence of the changes in the flow and the radius, as well as the delay between them, depended on the capacity and the status of the internal storage of water. It seems to be important how the resistance (R_{xs}) and the potential difference (ψ_x–ψ_s), determining the movement of the water between xylem and storage tissue, were related to the corresponding values determining the flow from soil into xylem. In the morning when transpiration started the water was easily withdrawn from saturated tissue. The radius of the stem then responded rapidly and sensitively. When R_{xs} increased and $|\psi_x$–$\psi_s|$ decreased in relation to the corresponding values of the inflow from soil, the exchange of water between xylem and store responded less sensitively to changes in the axial flow through the stem. The fluctuation in the stem size then became more attenuated and uncoupled from transpiration.

Figure 7 schematically outlines idealized diurnal courses of the flow through the stem and the change in its radius. Although diurnal courses varied from day to day in dependence on the weather, five characteristic phases may be distinguished. The first describes the nightly period of the stem's resaturation with water. There is no or little measurable flow. The internal stores replenish, and the radius increases, although the rate of this increase may become small towards the end of the phase. The second phase is one of a first delay. Usually it describes the delay between the increase of the flow and the shrinking of the stem. The sequence of the two, as mentioned above, may be reversed when the tree is saturated. Phase III is the period during which the stem shrinks most rapidly while the flow through it increases to its daily maximum. Phase IV describes the delay between the maximum in the flow and the minimum in the radius at its reversal point in the afternoon. The final and fifth phase is characterized by a decrease in the flow while the radius again increases. When the tree had transpired a lot during the day this period could last until early morning. The radius increases fastest at the beginning of

this period. Figure 8 shows the exchange of water between xylem and storage tissue during the five phases illustrated above. Water is withdrawn from the store most readily during phase III after the nocturnal resaturation (phases I and II). During phase IV withdrawal of water from the tissue becomes progressively restrained. At the beginning of phase V the exchange of water changes direction. It then moves back into storage tissue again. This takes place at the same rate of axial flow at which stored water moved in the opposite direction during phase III.

The diurnal behavior of the axial flow of water and its exchange between xylem and storage tissue suggests that towards the end of the fourth phase the store is exploited to such an extent that it is the large difference ψ_x–ψ_s which drives the water back to it during phase V. This would be enhanced by the simultaneous increase of ψ_x while transpiration decreases. However, the diurnal behavior of the changes in radius and axial flow, as shown in Fig. 2 for a sequence of wet and dry days, indicates a more complex situation. During the consecutive daily shrinking cycles of the stem its radius progressively decreased. The ΔS_d remained almost unaffected by this gradual decrease, although it would be expected to diminish as the stem loses water. Such independence of the daily oscillation of the radius from the fluctuation over several days could be explained by the presence of different types of internal stores for water. One type would be depleted and recharged in the daily cycle, whereas the other would undergo cycles over more than 24 h. Also, the osmotic potential of the sap within storage tissue might play a role. A drop of this potential, e. g. within phloem, during assimilation at daylight would increase ψ_x–ψ_s and thereby contribute to drive water back to the storage tissue. Because of the time constant for the daily exchange of water between xylem and store, daily minima of water potentials in the store may still remain larger than those in the xylem (Powell and Thorpe 1977).

The daily oscillation of the radius remained over considerable terms almost unaffected by the gradually changing water content of the stem. The ΔS_d then represented Q_d fairly well (Fig. 4a). However, if all periods of both years are considered then ΔS_d slightly increased relative to Q_d

when this was small. This may be responsible for the deviations in our estimates of sap flow (Table 1). The linearity between ΔS_d and Q_d was affected most when the tree was well saturated, although not in a sensitive way as seen in Fig. 2. Parlange et al. (1975) proposed a non-linear diffusion model to explain swelling and shrinking of phloem. According to their model, water moves more readily within the phloem as this becomes wetter. This effect, together with the moisture characteristics and the elasticity of the tissue, may contribute to the non-linearity of the relationship between ΔS_d and Q_d (cf. also Fig. 6). Katz et al. (1989) measured the remarkable ability of twigs of Norway spruce to take up intercepted water. The water sprayed onto 3- to 7-year-old twigs was absorbed through the bark and moved along radially oriented ray tissues into the xylem. As a consequence the water potential in the xylem recovered with a half-time of 50 min. A quick recovery in water potential, after the crown had been wetted, was also observed in experiments made in the field, where mature Norway spruce trees were exposed to drought in the soil (Grote and Dohrenbusch 1993; K. Herzog, unpublished data). It is not known how much the water taken up in this way contributes to transpiration. However, when the crown is frequently wetted it might be an alternative source for transpiration. Thus, the increase of ΔS_d relative to the small Q_d during wet weather might reflect some transpiration of water from aerial uptake.

The hysteretic relationship between ΔS_n and Q_d might result from an enhanced water uptake after days with large Q_d on which internal stores had been depleted (Fig. 4b), but there were additional factors such as water potential and soil temperature which influenced ΔS_n. Furthermore, during wet weather the stem grew in spurts – possibly also resulting from preceding large assimilation – which interfered with ΔS_n (cf. Fig. 3).

Kozlowski and Winget (1964) found that the daily shrinkage of stems of different species varied seasonally. They measured small shrinkages at the beginning and towards the end of season and found the maximal shrinkage to occur in the middle of it. Such a seasonal fluctuation in daily shrinkage might result partly from a changing availability of water in the soil. However, the seasonal course in the evaporative demand of the atmosphere might also contribute to it (cf. Hinckley et al. 1978). Von Wilpert (1990) reported that the diameter of the stem of Picea abies changed most on days when the tree was slightly stressed by drought in the soil. He argued that as long as there was enough water available the diurnal uptake of it could keep up with transpiration and so prevent the stem from much shrinking. On the other hand, the swelling of the stem would be suppressed during severe drought, because internal stores could not then be recharged. He concluded that the availability of water in the soil would have a major effect on the shrinkage of stems. There seems to be evidence that the shrinkage decreases as drought progresses in the soil, although it was not substantiated by our measurements because water never became short, but ΔS_d did not decrease in response to improved water availability. On the contrary, it appeared to be largest when tree and soil

were freshly resaturated. This suggests that even if water is plentiful, its diurnal uptake is still limited by the resistance of absorption. Hence, in spite of a large water potential in the soil, a substantial temporary deficit may arise within the tree during transpiration. Running (1980) reported a similar finding. He described a considerable limitation in the uptake of the water for Pinus contorta. Wronski et al. (1985) also concluded from their calculations that water withdrawn in one day from the internal stores of Pinus radiata might not be rechargeable over the diurnal time scale.

During 3 weeks with alternating wet and dry weather the ΔS_d – independent of the height of the stem at which it was measured – was less correlated to Q_d measured at the base than to the daily flow at half of the stem height (Herzog et al. 1994). This is explained by the water stored within the tree – including that causing size fluctuations – which functions as a buffer between transpiration and uptake. The time constant of the uptake of water from soil is larger than that of its withdrawal from internal tissues (cf. Nobel 1983). Thus, the uptake of water by large trees may lag considerably behind transpiration, and the time pattern of daily transpiration may better be represented by the shrinkage of the stem than by the daily flow into it.

The assessment of the transpiration of trees in the subalpine climate is difficult. Since crowns are periodically wet an approach at the leaf level is not advisable. The therefore sap flow may be inside the stems traced. However, this approach may also end up as a pure methodical adventure (cf. Herzog 1995). The fluctuation in stem size can be measured accurately with little destruction and expense compared to the measurement of sap flow. It enabled us to estimate the flow through xylem during different periods within a reasonable range of error compared to the flow obtained by heat balance. The stem size additionally reflected the time pattern of daily transpiration and the degree of water saturation in a sensitive way. The analysis of size fluctuations appears to be suitable to supplement or partly replace the measurement of the flow if conditions allow it.

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