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Diurnal variation in stem radii and transpiration flow at different crown levels of a Norway spruce (*Picea abies* (L.) Karst.)

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Synopsis
Diurnal fluctuations of stem radii and transpiration flows were recorded simultaneously at different crown levels of a subalpine Norway spruce. Daily oscillations of the stem radius at mid-crown level showed minimal amplitudes, and compared to those at the crown top a delay of more than 1 hour. Radius fluctuations over several days and the ratio $F_{base}/F_{mid\text{-}crown}$ (daily xylem flow at 3.3 m/daily flow at 15.6 m) reflected depletion and replenishement of tree-internal water storage. On days of water storage depletion, the comparison of the daily xylem flow balances (F_{base} - $F_{mid\text{-}crown}$) with the changes of the stem volume suggests that water is withdrawn also from other organs than the stem. The relationships between diurnal amplitudes of radius variation and daily xylem flows of the corresponding crown levels showed a remarkable hysteresis at the stem base. Therefore, the time dynamics of daily amounts of tree transpiration are better represented by diurnal dendrographic amplitudes than by daily xylem flows at the stem base. The transpiration of lower crown layers was strongly influenced by crown water interception.

Stammradius, Tagesgang, Xylemfluß, Wärmebilanz, Wasserspeicher, Transpiration, Kronenschichten, Picea abies.
Stem radius, diurnal, xylem sap flow, heat balance, water storage, transpiration, crown layers, Picea abies.

1. Introduction

Water relations of trees have often been addressed by micrometeorological methods (e. g. SPITTLEHOUSE & BLACK 1981) or by destructive sampling at selected times (e. g. TURNER 1981). Using non-destructive methods such as continuous dendrography and measurement of xylem sap flow, it is possible to analyze the water relations on the scale of a single tree crown, while also gaining useful information about water dynamics. Some results from a simultaneous application of the two methods are presented here.

2. Material and Methods

A healthy, codominant 221-year-old Norway spruce tree growing at the subalpine research station Seehornwald (STARK & al. 1991) near Davos was studied during summer 1992. (Tree height: 25 m, diameter at breast height: 36 cm, total needle area: 450 m^2 [HÄSLER & al. 1991]).
Dendrographs were mounted at three stem heights: 1.9 m, 11.8 m and 19 m. They consisted of precision displacement transducers (TRANS-TEK, Ellington, CT, USA) on metallic frames, anchored 50-mm deep into the hydroinactive xylem. To eliminate hygroscopic bias, the contact points of the transducers were placed 5-mm deep into the bark.
Flow rates of xylem sap were assessed by the method of stem tissue heat balance (ČERMÁK & al. 1973, ČERMÁK & KUČERA 1981, PEARCY & al. 1989). Flow meters (Gröger S.E.P., Bayreuth) were mounted at stem heights of 3.3 m and 15.6 m. Under steady-state conditions an input of heat energy (P) into the xylem tissue is equivalent to the heat losses by mass flow (Q_m) and conduction (Q_c). The temperature of the measured tissue sector was constantly held 1 K above the temperature of the surrounding tissue. The non-linear relationship between P and Q_m and the dependence of Q_c on changed thermal conductivities of tissues at different stem positions made bias corrections necessary. Correction parameters were assessed by laboratory measurements on a sap flow simulator and by parallel field measurements on the same stem. Zero-values were determined as mean values between 2 and 4 am each day. Daily sap flows were calculated as the amounts between 0 and 24 h.

3. Results and Discussion

The dendrograph in the mid-crown section (11.8 m) measured a daily oscillation, delayed and attenuated compared to those measured above and below (Tab. 1, Fig. 1). Three superimposed changes of stem radii over different time spans could be distinguished: a) a daily oscillation, strongly dependent on transpiration conditions; b) fluctuations over several days, representing changes of stem water storage; c) a still increasing seasonal trend, although radial growth had mainly been completed.

Tab. 1: Mean phase shifts, diurnal and nocturnal amplitudes of fluctuations of stem radii at different crown levels between June 27 and July 14 1992.

Tab. 1: Mittlere Phasenverschiebung, Tages- und Nachtamplituden der Radiusschwankungen auf verschiedenen Kronenhöhen zwischen dem 27. Juni und 14. Juli 1992.

Stem height	Expo-sition	Stem diameter	Mean phase shift [1]	Diurnal amplitude [2]			Nocturnal amplitude[3]		
				min	max	mean	min	max	mean
m		cm	min	µm	µm	µm	µm	µm	µm
19	W	14	-	0.37	17.87	9.84	3.18	20.60	10.83
11.8	W	26.3	-62.6 ± 0.3	0.30	9.45	5.38	1.33	11.30	5.59
1.9	W	36.9	-31.6 ± 0.2	0.44	11.52	7.49	2.22	13.36	8.57

[1] calculated by cross correlation analysis. Time lags ± SD of maximal correlation in relation to highest stem position.
[2] diurnal amplitude of July 11 is not defined.
[3] nocturnal amplitudes of July 10 and 11 are not defined.
[2,3] sensor accuracy: $< \pm 0.63$ µm.

Radius variations are known to be influenced by stem internal factors (e. g. stem elasticity, effective radius measured, phloem thickness) and environmental factors (e. g. soil moisture availability, air evaporativity, crown intercepted water) (KOZLOWSKI & WINGET 1964, PARLANGE & al. 1975). They were found to result mainly from shrinkage and swelling of the phloem, driven by internal forces of xylem water potential (MOLZ & KLEPPER 1973, JARVIS 1975).
The oscillations showed a characteristic saw-tooth pattern with decreasing slopes during the daytime (determined by transpirational demand, highly sensitive to climatic events) and curved increases during the night (determined by conditions of water uptake) (Fig. 1). The patterns of diurnal amplitudes of all dendrographs followed the courses of daily sap flows at the mid-crown level (Fig. 2). At stem base the relationship between the diurnal amplitudes and the daily sap flows showed a considerable hysteresis (Fig. 4 and 5).
In the alternating sequence of sunny and wet weather, days following a sunny period (July 4/5 and 11) showed a considerably increased ratio $F_{base}/F_{mid\text{-}crown}$ (daily flow at 3.3 m/daily flow at 15.6 m) (Fig. 3). The tree then was recovering from a depletion in its water reserves. This was intensified the first time (July 4 and 5) after a period of pronounced water depletion (cf. Fig. 1: decreasing trend in dendrograph records at the end of June). A significant capacity of internal water storage was indicated by the fact that at the lower stem position daily flows still decreased from June 5 to 6 and from June 11 to 12, whereas flows at the upper position already increased (Fig. 2). The refilling of the water storage generally took more time than the depletion. Dendrographic records described periods of progressive saturation readily extending over two days (Fig. 1: July 4 to 7 and 10 to 12).
After tree water storage had been refilled, $F_{base}/F_{mid\text{-}crown}$ became < 1 (Fig. 3: July 6 and 12). On these days, the stem flow at 15.6 m exceeded the flow at 3.3 m (Fig. 2), i. e. the tree water storage was depleted, although transpiration still remained low. Rises in flow rates at stem base lagged considerably behind those at mid-crown level (Fig. 1). Daily xylem flow balances (F_{base} - $F_{mid\text{-}crown}$) of the two days yield a water depletion of 1.1 kg and 0.9 kg (July 6 and 12), whereas the stem volume of the corresponding section can be estimated to have been reduced by only 1.8 cm^3 and 15.6 cm^3, respectively. This suggests that water had been withdrawn also from other storage locations than the stem (e. g. branches, needles).
The character of a wet to dry weather transition became evident in the period between July 12 and 15. The daily flows at both levels showed a progressive increase and divergence (Fig. 2). The divergence, similar as on days of tree resaturation, caused $F_{base}/F_{mid\text{-}crown}$ to increase (Fig. 3), but this time resulted from a gradually enhanced transpiration of the lower crown layers, while externally stored water (intercepted by the crown) was being removed. At the same time also the internal water storage was being reduced (Fig. 1: dendrograph records from July 12 to 15). Days with rain, even of only small amounts, were characterized by a small divergence of daily sap flows at the two stem positions (Fig. 2: July 7 to 10). Conditions of rain interception prevented the lower crown from transpiring.

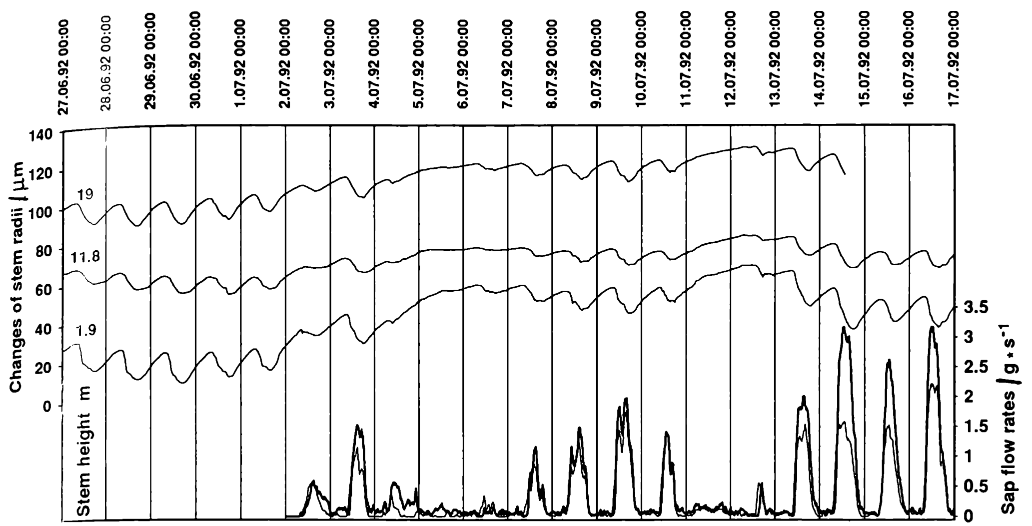

Fig. 1

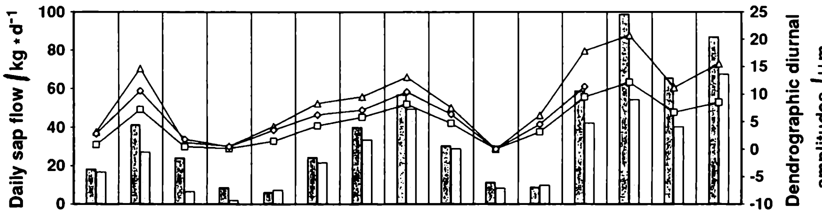

Fig. 2

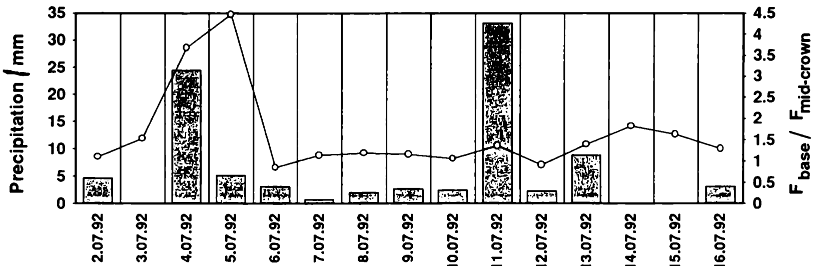

Fig. 3

Fig. 1: Top: Dendrographic records of the three crown levels: 19 m (top line), 11.8 m (middle line), 1.9 m (lowest line). Bottom: Daily courses of sap flow rates at the two crown levels: 15.6 m (thin line), 3.3 m (thick line).

Fig. 2: Daily sap flows measured at 15.6 m (light columns) and 3.3 m (dark columns). Dendrographic diurnal amplitudes at 19 m (standing squares), 11.8 m (lying squares), 1.9 m (triangles).

Fig. 3: Daily amounts of rain (columns) and ratios of basal to mid-crown daily sap flow ($F_{base}/F_{mid\text{-}crown}$) (circles).

Abb. 1: Oben: Dendrographische Aufzeichnungen auf den drei Kronenhöhen: 19 m (oberste Linie), 11,8 m (mittlere Linie), 1,9 m (unterste Linie). Unten: Tagesgänge der Saftflussraten auf den zwei Kronenhöhen: 15,6 m (dünne Linie), 3,3 m (dicke Linie).

Abb. 2: Tägliche Saftflussmengen, gemessen auf 15,6 m (helle Säulen) und 3,3 m (dunkle Säulen). Dendrographische Tagesamplituden auf 19 m (stehende Quadrate), 11,8 m (liegende Quadrate), 1,9 m (Dreiecke).

Abb. 3: Tägliche Niederschlagsmengen (Säulen) und die Verhältnisse der basal und in der Kronenmitte gemessenen täglichen Saftflussmengen ($F_{base}/F_{mid\text{-}crown}$) (Kreise).

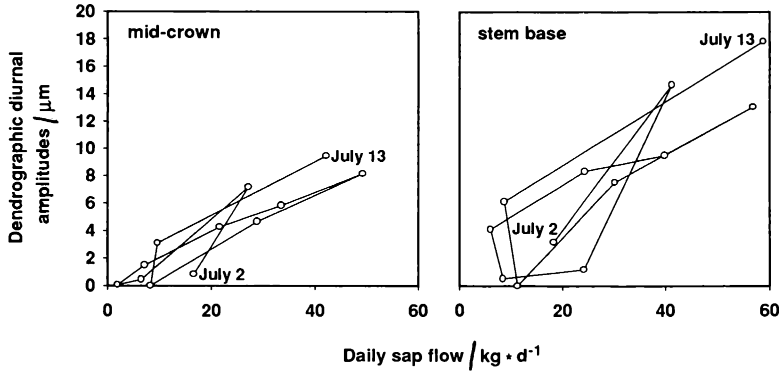

Fig. 4

Fig. 5

Fig. 4: Relationship between daily sap flows (at 15.6 m) and dendrographic diurnal amplitudes (at 11.8 m) in the mid-crown section. Period from July 2 to 13 1992.

Fig. 5: Relationship between daily sap flows (at 3.3 m) and dendrographic diurnal amplitudes (at 1.9 m) at the stem base. Time period as in Fig. 4.

Abb. 4: Beziehung zwischen täglichen Saftflussmengen (auf 15,6 m) und dendrographischen Tagesamplituden (auf 11,8 m) im mittleren Kronenbereich. Messperiode vom 2. bis zum 13. Juli 1992.

Abb. 5: Beziehung zwischen täglichen Saftflussmengen (auf 3,3 m) und dendrographischen Tagesamplituden (auf 1,9 m) bei der Stammbasis. Messperiode wie in Fig. 4.

4. Conclusions

Patterns, amplitudes and phase relations of continuous dendrographic readings are sensitive parameters for single-tree studies of water relation dynamics. The time pattern of daily amounts of tree transpiration is better represented by diurnal dendrographic amplitudes than by xylem flows at the stem base (hysteresis).

On days following replenishment of the tree water storage, daily sap flow at mid-crown level can exceed basal flow. Internal water storage (located also in other organs than the stem) is depleted then to a certain extent even at moderate transpiration.

Recovery of trees from water depletion may take several days and only occurs during periods of low daily transpiration.

In contrast to the upper crown, transpiration of the lower crown layers is strongly affected by water interception.

The occurrence of nightly conditions with no sap flow through the basal stem section of tall trees is questionable after periods of high diurnal transpiration. As a consequence zero-calibration of flow meters during the night time (as done in this study) might lead to an underestimation of the measured sap flows.

The method of stem tissue heat balance needs further improvement if it is to be used for quantitative sap flow determinations.

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