

Link between diurnal stem radius changes and tree water relations

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Summary Internal water reserves are depleted and replenished daily, not only in succulent plants, but also in trees. The significance of these changes in tissue water storage for tree water relations was investigated by monitoring diurnal fluctuations in stem radius.

In 6-year-old potted Norway spruce (*Picea abies* (L.) Karst.) trees, whole-tree transpiration rate (T), sap flow at the stem base and fluctuations in stem radius were measured at 10-min intervals over eight successive weeks. The dynamics of diurnal water storage in relation to the daily course of water movement was simulated and the contribution of stored water to T quantified.

The finding that, in *P. abies*, the course of bark water content is linearly coupled to stem radius fluctuations provided the basis for linking stem radius changes to a functional flow and storage model for tree water relations. This model, which consists of physical functions only and is driven by a single input variable (T), accurately simulates the diurnal course of changes in stem radius and water storage of the tree crown and stem. It was concluded that fluctuations were mainly determined by the course of transpiration. The availability of soil water and the degree to which storage tissues were saturated were also factors affecting the diurnal course of stem radius changes. Internally stored water contributed to daily transpiration even in well-watered trees, indicating that stored water plays an important role not only during periods of drought, but whenever water transport occurs within the tree.

Needle and bark water reserves were most heavily depleted during transpiration. Together they supplied approximately 10% of daily T on sunny days, and up to 65% on cloudy days. On a daily basis, the crown (mainly needles) contributed approximately eight times more water to T than the stem (mainly bark). The depletion of the two storage pools and the water movements observed in the trees always occurred in the same sequence. In the morning, T first caused a depletion of the water stored in the crown. It then caused depletion of bark storage tissues at ever increasing distances from the needles. Up to 75% of the transpired water could be withdrawn from storage tissues when the increase in T reached a maximum.

Keywords: dendrometer, *Picea abies*, sap flow, water storage model.

Introduction

Tissue water storage is an important factor in tree water relations. It is accessible to the individual tree only, unlike soil water, which may be taken up by other plants or lost through evaporation or drainage. When investigating the role of tissue water reserves on tree water relations, it is essential to (i) work with a functional flow and storage model that distinguishes between different storage locations, and (ii) use methods that allow continuous measurement of the diurnal dynamics of tissue water contents.

Zimmermann (1983) suggested a physical model with three water storage locations within the tree: the sapwood, the cell walls and the inactive vessels of the xylem (capillary water), and the living cells, e.g., the phloem of the bark or the mesophyll of needles. The respective characteristics of each compartment depend on how much water can be withdrawn under particular conditions (Siau 1984). Evaluation of the different storage compartments is controversial and based, in some cases, on methodological approaches that fail to distinguish between available and unavailable internally stored water. "Available" here means that the respective water reserves can be depleted within the natural range of xylem water potentials and can, therefore, contribute to whole-plant transpiration throughout the day.

One method of continuously observing diurnal depletion and refilling of stem water reserves is to measure stem radius changes. Among other authors, Whitehead and Jarvis (1981) and Landsberg (1986) have suggested in theoretical approaches that the diurnal stem radius fluctuations are coupled to tree water relations by changing water potential gradients within the tree. However, they give no applicable theory how the diurnal course of stem radius fluctuations is to be interpreted in terms of changing amounts of internally stored water or in terms of the general plant water status. Also, few studies have been made on the diurnal sequence of storage depletions (Loustau et al. 1996, 1998). Zweifel et al. (2001) showed that changes in the stem radius of young *Picea abies* (L.) Karst. trees are proportional to the water content in the bark and that the water content of the wood remained unchanged for xylem water potentials (Ψ_s) above -2.3 ± 0.3 MPa. A decrease in the sapwood water content occurs only when the critical limit for

cavitation is reached (Edwards and Jarvis 1982, Grace 1993, Jackson et al. 1995, Sherwin et al. 1998, Borghetti et al. 1998), which in the case of *P. abies* is approximately -2.5 MPa (Lu et al. 1996). Consequently, for Ψ_s above -2.3 ± 0.3 MPa, the water content of the bark can be continuously monitored with dendrometers (Herzog et al. 1995) because no water is withdrawn from inelastic tissues.

In the present work we developed a functional flow and storage model, which relates stem radius fluctuations to tree water relations, based on physical relationships. In contrast to existing models (Edwards et al. 1986, Tyree 1988, Früh 1995), which operate with a complex tree architecture, our model allows for only two storage pools (stem and crown) and two identical flow path sections. The model is driven by measurements of whole-tree transpiration (T). The results predicted by the model were compared with the changes in stem radius (bark water storage) and sap flow at the stem base of the potted *P. abies* trees. In this way, it was possible to verify directly the model output of stored water exchange by measurements and to estimate the contribution of internal stored water to transpiration and its implication for tree water relations. We discuss the meaning of diurnal stem radius fluctuation for tree water relations, the sequence of internal storage processes, the pattern of depletion and replenishment and the contribution of different storage pools to transpiration.

Material and methods

Sample trees

Three 6-year-old saplings of Norway spruce (*Picea abies* (L.) Karst.) were grown outdoors in a nursery in pots (volume 13 l; substrate: 30% (by weight) peat, 70% wood-fiber substratum; fertilizer: Osmocote plus 3 g l⁻¹, horn meal 3 g l⁻¹; pH ~4.5). During the experiment, the trees were kept for 8 weeks in the laboratory in front of an east-facing window. The most important tree dimensions are shown in Table 1. The soil matric water potential in the pots was measured by syringe-type tensiometers (Ballmoos, Horgen, Switzerland) (Marthaler et al. 1983) and was always kept above -10 kPa. Air relative humidity varied from 30 to 40% and air temperature varied from 20 to 23 °C. Wood growth was negligible during the experiment. Only tree C formed one new layer of xylem cells (< 15 μm).

Installation of the measuring instruments

The potted trees were placed, in rotation, for 7 days on a 30-kg (± 1 g) electronic balance (PM30-K, Mettler, Switzerland) (Figure 1). Pots were sealed with plastic film and covered with aluminum foil to prevent evaporation from the soil and to minimize heating by direct sunlight. Every third day the pots were uncovered for 12 h to allow air exchange.

Xylem sap flow was continuously monitored with a heat balance gauge (SGB 25, Dynamax Inc., Houston, TX) at the base of each stem. We followed the procedure for mounting and handling the stem heat balance gauges described by Herzog et al. (1997) with one modification: the silicon layer

Table 1. Characteristics of three 6-year-old Norway spruce (*P. abies*) trees studied during the periods indicated.

	Tree A	Tree B	Tree C
Height (m)	1.18	1.12	1.16
Stem diameter at the base (mm)	29.2	28.1	26.9
Stem volume (cm ³)	311	274	265
Needles dry (fresh) weight (g)	199 (615) ¹	188 (564)	165 (493)
Measurement period	15/09/96 to 07/11/96	18/01/97 to 10/03/97	18/01/97 to 10/03/97

¹ Estimated from stem size and needle dry weight.

between the thermocouples and the stem surface was separated from the bark by a thin layer of plastic film, to preclude possible damage to the bark from the silicon compound (Wiltshire et al. 1995).

A point dendrometer was mounted on the stem of each tree. The dendrometers, consisting of a precision displacement transducer (TRANS-TEK, Ellington, CT) and a body of stainless steel, provided continuous measurements of the stem radius (Herzog et al. 1995). The dendrometer body was fixed on two sides to the pot. The sensing head was glued with tar to the surface of the stem between the sap flow gauge and the lowest twigs. The resolution of the dendrometers was 1.5 μm .

Stem radius and sap flow rates were measured at 5-s intervals, averaged every 10 min and recorded with a data logger (CR7, Campbell Scientific, Logan, UT). The weights of the potted trees were recorded automatically every 10 min.

Model

The flow and storage model was developed to simulate the water relations and the stem radius fluctuations with a given daily course of transpiration as the only input. The model comprises two types of elements: storage pools and flow path sections. Storage pools are characterized by a direct link between the water content (P_{Pool}) and the water potential (Ψ_{Pool}), described by their desorption curves, $\Psi(P)$. The soil is considered a non-limiting storage pool with a constant matric water potential of -5 kPa, which serves as a boundary condition. The translocation of water in the flow path sections follows Darcy's law.

The model contains two storage pools: the crown storage pool (shoot without stem, mainly the needles) and the elastic stem storage pool (mainly the bark). The water content of the xylem is assumed to be constant (Zweifel et al. 2001). The crown storage is located at the top of the model tree and the stem storage is assumed to be in the middle of the stem. Two flow paths connect the storage pools with one another. One flow path is located between the storage pools mentioned above and the other between the stem storage and the soil, both with equal flow resistance (R_{Xylem}). Figure 1 illustrates the corresponding elements of the constellation and the model input and outputs. The transpiration rate (T) is the driving force of

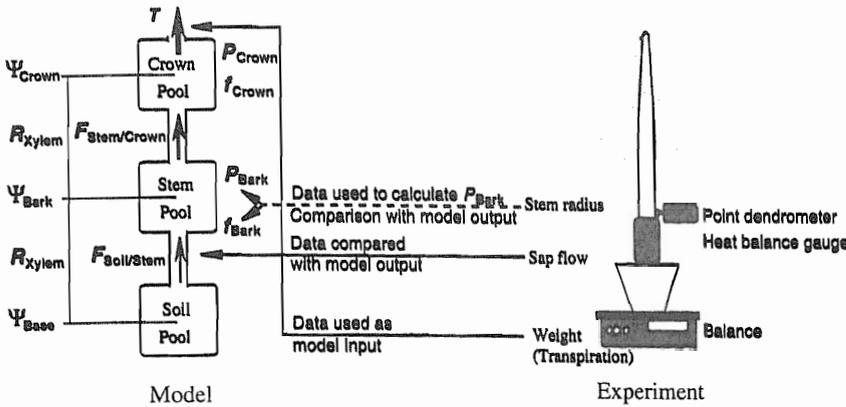


Figure 1. Model (left) and corresponding measurements. The model consists of two internal storage pools (crown and stem), one external source (soil) and two flow path sections with identical resistance. Measurements were taken with a dendrometer (stem radius fluctuation), a stem heat balance gauge (sap flow) and a balance (transpiration). Parameter T = transpiration, $F_{Soil/Stem}$ = flow rate at the stem base, P_{Bark} = water content of the elastic stem storage pool, P_{Crown} = water content of the crown, f_{Bark} = flow rate out

of the elastic stem storage, f_{Crown} = flow rate out of the crown, $F_{Stem/Crown}$ = flow rate in the upper stem section, Ψ_{Base} = constant soil matric water potential, Ψ_{Bark} = water potential in the middle of the stem, Ψ_{Crown} = leaf water potential and R_{Xylem} = resistance of the flow path.

water transport, which at first affects the water content of the crown storage pool (P_{Crown}). As a consequence, a water potential gradient develops between the storage pools and water flow is induced in the upper flow section ($F_{Stem/Crown}$), causing depletion of the elastic stem storage (P_{Bark}). A water potential gradient also develops between the stem storage compartment and the soil, causing water flow in the lower flow section ($F_{Soil/Stem}$). The depletion rates of the storage pools, f_{Crown} and f_{Bark} , are equivalent to the first derivatives of the water content of the respective pools:

$$f_{Crown} = \frac{\Delta P_{Crown}}{\Delta t},$$

$$f_{Bark} = \frac{\Delta P_{Bark}}{\Delta t}.$$

Model equations

A. Desorption curves For both storage pools (crown and bark) the same function is used for the relationship between water content and water potential (Zweifel et al. 2001), but with different parameters k_1 and k_2 (Figure 2):

$$\Psi_{Crown}(P_{Crown}) = \frac{\Psi_{Crown\ min}}{\exp\left(\frac{-k_1\ Crown + P_{Crown}}{k_2\ Crown}\right) + 1}, \tag{1}$$

where P_{Crown} is the available water of the crown (g), Ψ_{Crown} is the water potential of the crown (MPa), $\Psi_{Crown\ min}$ is the minimum of Ψ_{Crown} (MPa), $k_1\ Crown$ is the amount of stored water at the point of inflection of $\Psi(P)$ (g) and $k_2\ Crown$ is the index for the slope of $\Psi(P_{Crown})$ at the point of inflection.

B. Equations for the unknown variables The flow rates in the two flow paths can be written as follows:

$$F_{Soil/Stem} = \frac{\Psi_{Base} - \Psi_{Bark}}{R_{Xylem}}, \tag{2}$$

where $F_{Soil/Stem}$ is the flow rate at the stem base ($g\ h^{-1}$), Ψ_{Bark} is the water potential of the stem storage (MPa) and the xylem water potential in the middle of the stem (MPa), Ψ_{Base} is the xylem water potential at the stem base (MPa) and R_{Xylem} is the resistance in the flow path ($MPa\ h\ g^{-1}$).

$$F_{Stem/Crown} = \frac{\Psi_{Bark} - \Psi_{Crown}}{R_{Xylem}}, \tag{3}$$

where $F_{Stem/Crown}$ is the flow rate in the upper flow path ($g\ h^{-1}$). Equations 2 and 3 lead to:

$$F_{Soil/Stem} - F_{Stem/Crown} = f_{Bark} = \frac{\Psi_{Base} - 2\Psi_{Bark} + \Psi_{Crown}}{R_{Xylem}}, \tag{4}$$

where f_{Bark} is the depletion rate of the elastic stem storage ($g\ h^{-1}$). Thus the final equation for transpiration is:

$$T = f_{Crown} + F_{Stem/Crown}, \tag{5}$$

where T is the transpiration rate ($g\ h^{-1}$) and f_{Crown} is the deple-

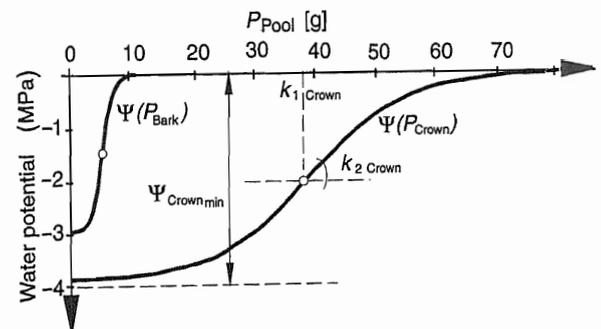


Figure 2. Idealized desorption curves $\Psi(P_{Bark})$ and $\Psi(P_{Crown})$ as derived from plant parts of the same experimental trees; P = water content of the storage tissue per tree, k_1 = amount of stored water at the point of inflection of $\Psi(P)$, k_2 = index for the slope of $\Psi(P)$ at the point of inflection and Ψ_{min} = minimum of $\Psi(P)$ (Zweifel et al. 2001).

tion rate of the crown storage (g h^{-1}).

Consequently, the four unknown variables in the model (Ψ_{Base} , Ψ_{Crown} , $F_{\text{Stem/Crown}}$ and $F_{\text{Soil/Stem}}$) can be calculated from Equations 2 to 5.

Calibration of the model

Three of the parameters used in the model are predetermined: Ψ_{Base} , $\Psi_{\text{Crown min}}$ and $\Psi_{\text{Bark min}}$. The xylem water potential at the stem base (Ψ_{Base}) was set at a constant value of -5 kPa, because in our experiment the trees were kept in wet soil and Ψ_{Base} was always near zero. The $\Psi_{\text{Pool min}}$ values for crown and bark were set at -4 and -3 MPa, respectively, slightly below the corresponding values given in the literature (e.g., Larcher 1995, Zweifel et al. 2001).

There are three adjustable parameters in the model: k_1 , k_2 and R_{Xylem} . The initial values for k_1 and k_2 for both storage pools were approximately known from previously measured desorption curves for trees treated in a similar way (Zweifel et al. 2001). The naturally occurring range of water potentials in well-watered *P. abies* (0 to -2.3 MPa) was used to find a base value for R_{Xylem} from which flow rates within the range of rates observed during measurements could be deduced.

The three parameters of the model were estimated by nonlinear regression by a least squares method. Both $F_{\text{Soil/Stem}}$ and P_{Bark} were chosen as qualified dependent variables to calibrate the model parameters, because they were measured by two independent methods. The absolute deviations between measured and simulated results for $F_{\text{Soil/Stem}}$ were weighted by a single factor to obtain a similar range of differences for $F_{\text{Soil/Stem}}$ as well as for P_{Bark} . The values for the model parameters were optimized by the Microsoft Excel 98 software package, which uses regression iteration steps. The physiological limits under natural conditions (the maximum water content of the storage pools, and the range of water potential within the xylem and in the crown) were taken into account in the optimizing process. The optimized parameters for each tree and the values derived from measured desorption curves are listed in Table 2.

Results

Experimental results

Diurnal dynamics of water relations The diurnal dynamics of water relations observed were similar for the three trees. Therefore, the data for tree B, shown in Figures 3–7, illustrate the processes in all three trees. The diurnal course of canopy transpiration and sap flow at the stem base (direct measurements), the course of the water content of the stem storage pool (correlated to the measured stem radius), and the diurnal course of the water content of the crown storage pool (calculated) are shown in Figure 3. A time lag between the increase in T and the onset of $F_{\text{Soil/Stem}}$ was observed in the morning almost every day. On sunny days, when transpiration was high, there was a shorter lag than on cloudy days with low transpiration. Examples for sunny and cloudy days are depicted in Figure 4. The time lag strongly corroborates the idea of a daily depletion

Table 2. Model parameters and measured values for the desorption curve of the two storage pools: the maximum water contents ($P_{\text{Pool max}}$) as derived from measurements, the minimum water potentials of the storage pools ($\Psi_{\text{Pool min}}$) as predetermined, and the parameters of the model (k_1 , k_2 , R_{Xylem}) as estimated by nonlinear regression with least squares for three potted *P. abies* trees. The measured values are derived from dehydration experiments with plant parts of the same trees (Zweifel et al. 2001).

	Tree A	Tree B	Tree C	Measured values
<i>Stem storage</i>				
$P_{\text{Bark max}}$ (g)	16.4	9.8	9.3	3.5
$\Psi_{\text{Bark min}}$ (MPa)	-3.0	-3.0	-3.0	-2.6
k_1 Bark	10.0	8.0	7.4	2.8
k_2 Bark	1.8	1.1	0.9	0.8
<i>Crown storage</i>				
$P_{\text{Crown max}}$ (g)	108.4	87.3	81.7	17.0
$\Psi_{\text{Crown min}}$ (MPa)	-4.0	-4.0	-4.0	-3.5
k_1 Crown	74.5	69.3	59.3	15.0
k_2 Crown	5.7	4.3	10.9	2.2
<i>Flow resistance</i>				
R_{Xylem} (MPa h g^{-1})	1.7	1.5	1.6	-

of internally stored water, and corresponds well with the shrinkage of the stem and the calculated decrease in the crown water content. Usually, the water reserves in the bark and crown were depleted in the morning and replenished within 24 h. On days with high transpiration and water-saturated storage tissues, the water balance became negative and the water deficit could last for several days (e.g., Figure 3; Days 3 to 6). The more stored water was depleted, the less it contributed to transpiration.

A synthesis of the measurements from several sunny days is shown in Figure 5. The diurnal sequence of the ecophysio-

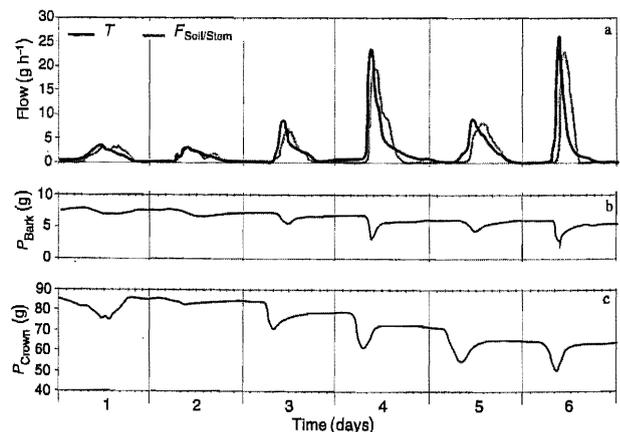


Figure 3. Measured: (a) transpiration rate (T), and sap flow rate at the stem base ($F_{\text{Soil/Stem}}$), (b) bark water content per tree (P_{Bark}) as derived from stem radius measurements, and (c) crown water content per tree (P_{Crown}) as calculated from T , $F_{\text{Soil/Stem}}$ and P_{Bark} .

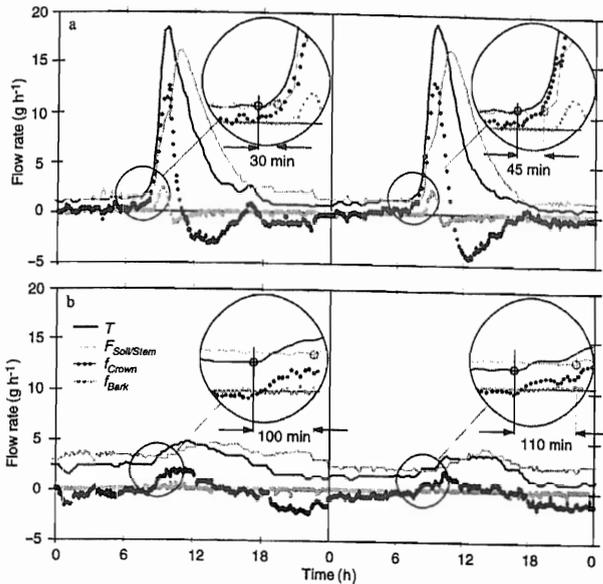


Figure 4. Measured water movement within a tree (a) on sunny days with high transpiration rates and (b) on cloudy days with low transpiration rates. The arrows indicate the respective onset of transpiration and sap flow at the stem base in the morning.

logical processes involved in water translocation and storage began in the morning with (1) an increase in transpiration and an immediate depletion of the crown pool; which was followed by (2) an increase in sap flow rate in the stem accompanied by the depletion of the elastic stem storage; (3) a peak in rate of tissue water depletion; (4) a peak in transpiration rate; (5) a peak in sap flow rate; and finally (6) the replenishment of tissue water reserves (Figures 5a and 5b). This sequence was the same every day, but the magnitude of the various processes varied, depending on the daily course of water losses from the foliage (Figures 3 and 4).

The maximum depletion rates of the storage pools ($f_{Bark\ max}$ and $f_{Crown\ max}$) occurred between the onset of $F_{Soil/Stem}$ and T_{max} (Figure 5c) and were derived as differences between the respective storage inputs and outputs:

$$f_{Crown} = T - F_{Stem/Crown},$$

$$f_{Bark} = F_{Stem/Crown} - F_{Soil/Stem}.$$

The proportions between T_{max} : $F_{Soil/Stem\ max}$: $f_{Crown\ max}$: $f_{Bark\ max}$ were about 7:6:3:1 (Table 3) and show that water was withdrawn from the crown storage three times as fast as from the elastic stem storage, but only half as fast as from the soil. This proportion also indicates the amount of available water in the two storage pools compared with the amount of water withdrawn from the soil. Replenishment of the storage pools began in the afternoon as soon as $F_{Soil/Stem}$ exceeded T . Usually the replenishment of the storage pools was slower than their depletion (Table 3). The replenishment of the storage pools lasted from the early afternoon until the next morning, about twice as

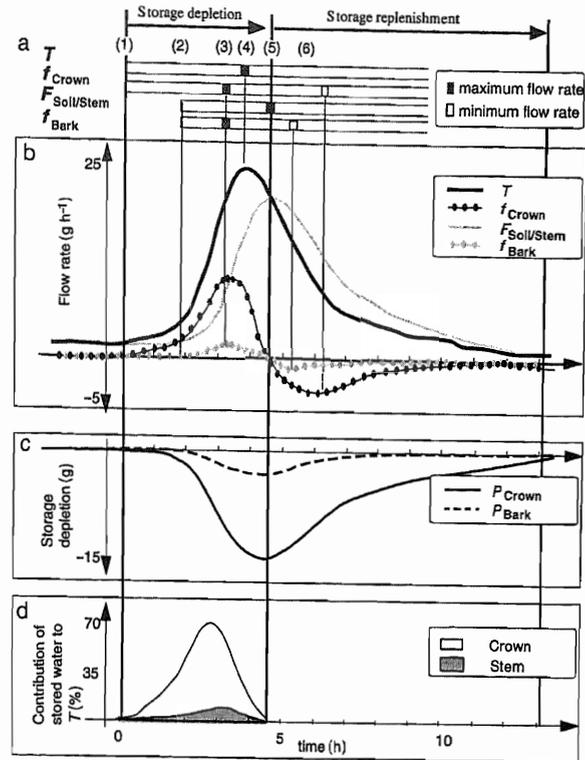


Figure 5. Synthesis of the results obtained with potted *P. abies* trees on several sunny days (the x-axis shows the time after the onset of transpiration in the early morning (Δt)). (a) Diurnal course: (1) increase of transpiration and depletion of the crown; (2) increase of the sap flow at the stem base, and depletion of the bark; (3) maximum flow rate out of storage tissues; (4) maximum transpiration rate; (5) maximum sap flow rate; and (6) replenishment of the storage tissues. (b) Tree water flow: T = transpiration; $F_{Soil/Stem}$ = flow rate at the stem base; f_{Crown} = depletion rate of the crown and f_{Bark} = depletion rate of the stem. (c) Water content of the two internal storage tissues P_{Crown} and P_{Bark} . (d) Contribution of internally stored water to transpiration.

long as storage depletion. During the night, T and $F_{Soil/Stem}$ never completely ceased, even when the internal storage pools were fully replenished.

Contribution of internally stored water to transpiration

The two storage pools were depleted daily during the morning and therefore contributed to transpiration over several hours. The contribution depended on the daily total amount of water transpired, which varied between 10 and 400 g. On sunny days, with a high transpiration rate, about 10% of the water transpired was directly withdrawn from internal reserves; on cloudy days the contribution rose to as much as 65% (Figure 8a). The maximum daily amounts of water that were withdrawn from internal reserves for transpiration within the 8-week study period are listed in Table 4. The crown always contributed 6 to 8 times more water to transpiration than the stem bark (Figure 8b).

The diurnal dynamics of internal water reserves for a sunny day are shown in Figures 5c and 5d. For such a day, with high transpiration rates, the daily contribution of the internal water

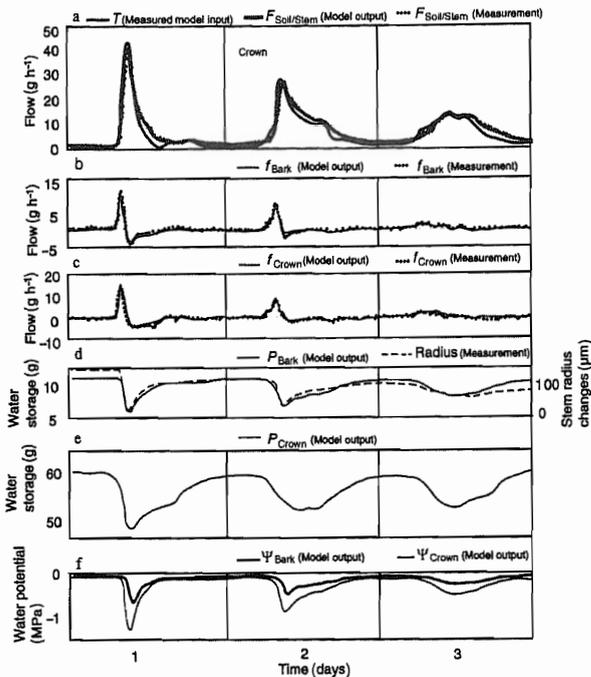


Figure 6. Model input, model output, and the corresponding measurements: (a) transpiration (T); the flow rate at the stem base ($F_{\text{Soil/Stem}}$); (b) depletion rate of the bark (f_{Bark}); (c) depletion rate of the crown (f_{Crown}); (d) water content of the stem storage per tree (P_{Bark}) and the corresponding stem radius changes at the base (right hand scale); (e) water content of the crown storage (P_{Crown}); and (f) xylem water potential at the middle of the stem (Ψ_{Bark}) and leaf water potential at the tree top (Ψ_{Crown}).

reserves to transpiration was only about 10%. Nevertheless, internally stored water played an important role in the morning when the transpiration rate began to rise. During that period, the depletion of tissue water exceeded $F_{\text{Soil/Stem}}$, and consequently crown and bark served as the main sources for transpiration. In the morning, the contribution of internally stored water to transpiration reached up to 75%.

To estimate the natural range of tissue water storage, the highest and lowest values within the 8-week study period were determined. For all trees, the maximum and minimum values were observed during a period of less than 2 weeks. This duration was of interest for estimating the impact of cell growth on stem radius fluctuations. During our experiment, cell growth was negligible. The differences between these extremes were defined by the storage capacity of the crown ($W_{\text{V Crown}}$) and bark ($W_{\text{V Bark}}$), respectively (Table 4). About 25% of the water localized in the needles and about 6% of the water in the stem (bark and wood) were potentially available for transpiration. Within 24 h, 30 to 50% of this stored water could have been totally exhausted or fully replenished.

Model results

The diurnal dynamics of the water balance of the young spruce trees could be simulated for a given course of transpiration and the tree-specific parameters listed in Table 2. Figure 6 shows the simulated rates for crown flow at the stem base and out of

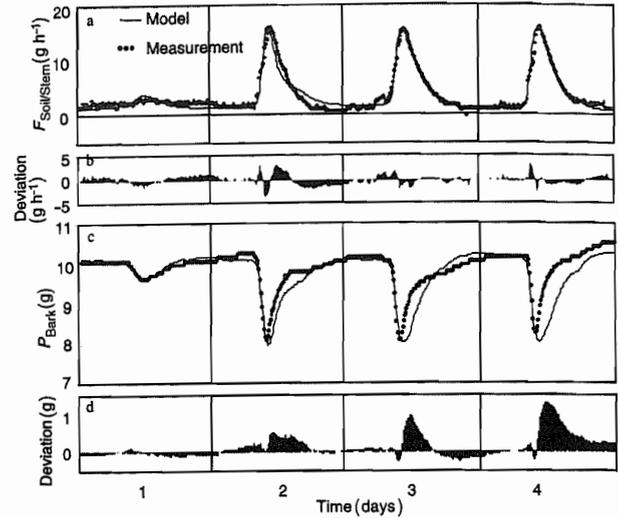


Figure 7. Deviation between the model output and measurements: (a) sap flow rate at the stem base ($F_{\text{Soil/Stem}}$) and (b) corresponding deviation; (c) stem water content (P_{Bark}) and (d) corresponding deviation. Day 1 was cloudy, whereas the following 3 days were sunny.

the storage tissues, and the water content of the storage pools on three successive days. The simulated flow rates, as well as the changes in the water contents, agree well with the measurements. No water potential readings were taken from the experimental trees and this part of the model output was not verified. The minimum water potential in the model output was lower in the crown than in the stem. The simulated water potentials Ψ_{Crown} and Ψ_{Bark} varied over the 8-week study period within a plausible range of -0.01 to -1.7 and -0.05 to -1.0 MPa, respectively.

Comparison of the results of the model with the measurements showed that the model gives a reasonable simulation of the actual water movement in the experimental trees (Figures 7a and 7c). Usually, the simulated flow rates differed only slightly from the corresponding measurements; the mean absolute difference between the calculated and measured $F_{\text{Soil/Stem}}$ was only 0.51 g h^{-1} (Figure 7b). However, the simulated course of the water content of the stem storage consistently differed from the measurements during the replenishment period. The onset of the simulated replenishment fitted well to the measurements, but the simulated maximum of the replenishment always occurred with a time lag during the recovery phase (Figure 7d). On average for the 8 weeks, the deviation during the replenishment phase was 150% higher than during the depletion phase. Nevertheless, the diurnal sequence of water movements and their maximum values were the same in the model output as in the measurements.

Discussion

Dynamics of stem radius fluctuations as an indicator of tree water relations

Internal water reserves in bark and needles are depleted and re-

Table 3. Maximum flow rates (g h^{-1}) measured on three *P. abies* trees.

	Tree A	Tree B	Tree C
Maximum transpiration rate ¹ , T_{\max}	45.6	27.8	33.3
Maximum flow rate at the stem base ¹ , $F_{\text{Soil/Stem max}}$	41.5	22.5	25.7
Maximum stem storage depletion rate ² , $f_{\text{Bark max}}$	5.8	4.3	3.1
Maximum stem storage replenishment rate ² , $f_{\text{Bark min}}$	-5.2	-4.6	-2.5
Maximum crown storage depletion rate ² , $f_{\text{Crown max}}$	16.8	12.9	9.6
Maximum crown storage replenishment rate ² , $f_{\text{Crown min}}$	-10.2	-16.0	-5.6

¹ Directly measured.

² Calculated from measurements.

plenished daily by changing water potential gradients within the plant (Whitehead and Jarvis 1981, Landsberg 1986). Our finding, that the course of the bark water content is linearly coupled to the stem radius fluctuations (Zweifel et al. 2001), provided a basis for linking the stem radius changes to tree water relations. With the help of a flow and storage model based on physical functions only, it was possible to simulate accurately the diurnal course of stem radius and bark water storage. The fluctuations were determined mainly by the course of transpiration, but also by the availability of soil water and the saturation of the internal storage tissues. This knowledge enabled us on the one hand to estimate the absolute amounts of internally stored water, and on the other hand to interpret the species-specific functionality of tree water relations; e.g., the maximum transport rates through the stem or the contribution of internally stored water to transpiration. This functionality, which is part of a tree's adaptation for survival, determines under what conditions trees of a certain species are able to grow and to compete with other plants.

Functionality of water storage usage and contribution to transpiration

The needles are assumed to be the main location of available water in the crown storage pool because the water content of the sapwood in *P. abies* does not change with changes in xylem water potentials above -2.3 ± 0.3 MPa (Lu et al. 1996, Zweifel et al. 2001). Within this range of xylem water potentials, the water in the tracheids moves to the crown and is transpired through the stomata, and must simultaneously be replaced by water from other storage locations. Consequently, this water cannot be exhausted by transpiration even though the sapwood contains the largest absolute amount of water within a tree (Jarvis 1975).

In young Norway spruce trees, internally stored water is withdrawn daily from the crown and bark. The percentage of available water from the respective total tissue water reserves is up to 25 and 6% for crown and stem, respectively. The contribution of internally stored water to transpiration depends on the amount of water transpired daily. It varies between 10 and 65% on a sunny and a cloudy day, respectively. Tyree (1988) reported similar values from model calculations for western red cedar (*Thuja occidentalis* L.). He found the contribution of internally stored water to transpiration to be between 20 and 40%, approximately 65% of this water being withdrawn from leaves. In our experiment, the crown storage contributed about 87% to the water withdrawn from the internal storage tissues. The sample trees discharged and replenished up to 50% of the available storage water within a day. The depletion of the stored tissues occurred within 4 to 8 h in the morning, and dur-

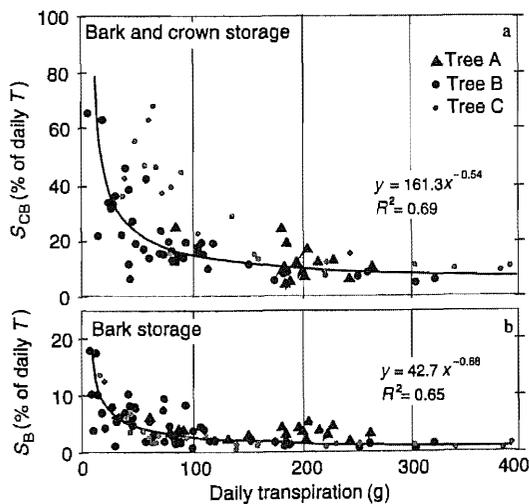


Figure 8. Daily contribution of stored water to transpiration: (a) crown and elastic stem storage together (S_{CB}); and (b) elastic stem storage alone (S_B). The measurements from Tree B were fitted by the functions presented in the figure (solid line).

Table 4. Maximum daily contribution to transpiration (g) of internally stored water ($W_{D \text{ Bark}}$, $W_{D \text{ Crown}}$) and the water storage capacity of bark and crown ($W_V \text{ Bark}$, $W_V \text{ Crown}$).

	Tree A	Tree B	Tree C
$W_{D \text{ Bark}}$	4.3	4.1	3.5
$W_{D \text{ Crown}}$	37.8	21.7	33.0
$W_V \text{ Bark}$	16.4	9.8	9.3
$W_V \text{ Crown}$	108.4	87.3	81.7
Bark water content	245	205	195
Crown water content	416	376	328

ing this period the contribution of internally stored water to transpiration reach up to 75% of the water transpired (Figure 5). In other words, during a short period in the morning on a sunny day, the contribution of stored water to transpiration can be higher than the amount of water drawn from the soil during the same period. This phenomenon was also suggested from model calculations of tree water relations by Edwards et al. (1986) and Tyree (1988).

The diurnal course of depletion and replenishment of stored water is closely related to the course of transpiration. An increase in transpiration rate leads to a rapid decrease in Ψ_{xylem} . The actual Ψ_{xylem} depends on the rate of depletion of tissue water reserves and on the amount of water withdrawn from the soil. The crown water content soon becomes reduced, even at low transpiration rates. The relationship between tissue water content, water flow and Ψ_{xylem} is compatible with the observed correlation between increasing sap flow rate and the simultaneous onset of bark-stored water depletion at the stem base. In agreement with findings for mature Norway spruce trees (Herzog et al. 1995, Loustau et al. 1998, Zweifel and Häslér 2000), we observed that tissues in young trees are depleted of stored water in sequence with increasing distance from the location of the water loss.

Physiological implications of internal water storage

The two main storage locations of the shoot (crown and bark) differ in importance in Norway spruce trees. The crown storage (mainly needles) seems to be quantitatively relevant for the daily transpiration of the young trees, whereas the stem bark seems to be of minor importance in accommodating differences between water uptake and loss. Following the suggestions of Edwards et al. (1986), we assumed that water released from the bark serves as an additional buffer to preclude low xylem water potentials that might otherwise be caused by peaks of transpiration. Therefore, the xylem water potential is smoothed along the flow path, which may help avoid xylem cavitation. Such a mechanism would enable the tree to bridge short transpiration peaks without stomatal closure. We conclude, therefore, that trees can use stored water to allow continued photosynthesis when transpiration exceeds soil water uptake.

The utilization of internal water reserves makes trees less dependent, in the short term, on soil water content. Even in well-watered soil the crown and stem water reserves are depleted every morning. Therefore, we conclude that the proportion of water stored in living tissues of the experimental trees was of only minor importance during drought periods. Holbrook (1995) stated that the water in an effective storage pool must be readily available when needed, but not so easily accessed that it is withdrawn before the onset of drought stress conditions. A release of the internally stored water in the experimental trees occurred every day, and consequently we assume that the diurnal release of stored water is a necessity for efficient water transport under normal conditions. Our experimental evidence does not indicate whether there is additional water stored for use during drought periods. Observed sea-

sonal changes in xylem water content (Waring and Running 1978, Waring et al. 1979) indicate the potential ability of certain tree species to use additional internal water reserves beside those in the crown and bark at low Ψ_{xylem} .

Comparison of the measurements and model output

The measurements of stem radius changes and sap flow rates were accurately simulated with a flow and storage model, which needs only a small number of parameters to optimize the output. Four of the five parameters could be derived from the desorption curves of the crown and stem. Even if these parameters were substituted by measured values and set proportionally for the estimated storage capacity, the model output fitted the measurements well. The simple structure of the model (linear tree architecture with only two storage pools, linked by identical flow path sections) did not have a negative effect on the result. In contrast to Tyree (1988) and Früh (1995), we suggest that a simple model without complex tree architecture can accurately simulate the diurnal dynamics of changes in stem radius and sap flow rates at the stem base, at least for young trees.

The only significant divergence between the model output and measured results was observed during the replenishment of stem bark water reserves. The model always simulated replenishment as occurring more slowly than the measurements showed (Figure 7). Hysteresis, because of a discrepancy between the sorption and desorption processes, is well known in soil sciences (Jury et al. 1991). In contrast to the slower depletion compared with replenishment in the tree, hysteresis in the soil shows a faster depletion (desorption) than replenishment (sorption). In the present model, this divergence is assumed to result from using the desorption curve for both the depletion and replenishment of water storage. Desorption curves were obtained by air-drying the plant parts (Zweifel et al. 2001), and the use of the results of the unidirectional flow seems to be unsuitable for simulating the bidirectional water exchange between the xylem and bark. A possible explanation for the accelerated replenishment process could be the increase in the osmotic potential of storage tissue cells during the day, which is caused by additional assimilates from the needles and their lowered water content. Thus, there could be an additional potential gradient to promote the withdrawal of water by the bark. However, it is possible that the discrepancy results from the simplified model structure.

Conclusions

The aim of this investigation was to simulate the daily physiological reactions of individual trees, namely stem radius fluctuations, tissue water storage dynamics and sap flow rates from the course of transpiration. The flow and storage model accurately simulates reality, and its physically based functions suggest an explanation of the interactions among the components of tree water relations on a physiological level. Our model may serve as a useful instrument for investigating the relationships between water storage pools, the sequence of in-

ternal water storage processes, the timing of the depletion and replenishment of stored water and the contribution of different storage pools to transpiration. Further investigations are needed to reverse the chain of cause and effect to interpret the dynamics of stem radius fluctuations with regard to their meaning for tree water status under normal conditions and under conditions of environmentally imposed stress.

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