Tree Physiology 27, 181–198

Tree water storage and its diurnal dynamics related to sap flow and changes in stem volume in old-growth Douglas-fir trees

JAN ČERMÁK,[1,2,3] JIŘÍ KUČERA,[4] WILLIAM L. BAUERLE,[5] NATHAN PHILLIPS[6] and THOMAS M. HINCKLEY[3]

[1] *Institute of Forest Ecology, Mendel University of Agriculture and Forestry, 61300 Brno, Czech Republic*

[2] *Corresponding author (cermak@mendelu.cz)*

[3] *College of Forest Resources, University of Washington, Seattle, WA 98195, USA*

[4] *Environmental Measuring Systems Inc., 61300 Brno, Czech Republic*

[5] *Department of Horticulture, Clemson University, Clemson, SC 29634, USA*

[6] *Department of Geography, Boston University, Boston, MA 02215, USA*

Received September 5, 2005; accepted April 1, 2006; published online November 1, 2006

Summary Diurnal and seasonal tree water storage was studied in three large Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees at the Wind River Canopy Crane Research site. Changes in water storage were based on measurements of sap flow and changes in stem volume and tissue water content at different heights in the stem and branches. We measured sap flow by two variants of the heat balance method (with internal heating in stems and external heating in branches), stem volume with electronic dendrometers, and tissue water content gravimetrically. Water storage was calculated from the differences in diurnal courses of sap flow at different heights and their integration. Old-growth Douglas-fir trees contained large amounts of free water: stem sapwood was the most important storage site, followed by stem phloem, branch sapwood, branch phloem and needles. There were significant time shifts (minutes to hours) between sap flow measured at different positions within the transport system (i.e., stem base to shoot tip), suggesting a highly elastic transport system. On selected fine days between late July and early October, when daily transpiration ranged from 150 to 300 liters, the quantity of stored water used daily ranged from 25 to 55 liters, i.e., about 20% of daily total sap flow. The greatest amount of this stored water came from the lower stem; however, proportionally more water was removed from the upper parts of the tree relative to their water storage capacity. In addition to lags in sap flow from one point in the hydrolic pathway to another, the withdrawal and replacement of stored water was reflected in changes in stem volume. When point-to-point lags in sap flow (minutes to hours near the top and stem base, respectively) were considered, there was a strong linear relationship between stem volume changes and transpiration. Volume changes of the whole tree were small (equivalent to 14% of the total daily use of stored water) indicating that most stored water came from the stem and from its inelastic (sapwood) tissues. Whole tree transpiration can be maintained with stored water for about a week, but it can be maintained with stored water from the upper crown alone for no more than a few hours.

Keywords: dendrometer, flow rate differences, heat balance method, time shift, tissue free water content, vertical profile.

Introduction

Most analyses of plant water relations regard the soil as the sole source of transpired water. Roberts (1976) reported that the amount of free water from storage in *Pinus sylvestris* L. trees and stands is insignificant relative to daily or seasonal transpiration. Similarly, Tyree and Yang (1990) concluded that stored water is not a significant source of water for transpiration in most woody plants. Holbrook (1995) in her review of stem water storage stated: "Its [Stem water storage] role in maintaining high levels of photosynthetic carbon gain during periods of drought, however, is limited to plants with inherently low transpiration rates (i.e., CAM succulents and perhaps large conifers)." However, Ladefoged (1963), Hinckley and Bruckerhoff (1975), Waring and Running (1978), Waring et al. (1979) and Čermák et al. (1976, 1982) have suggested that internal water storage in both elastic and inelastic tissues may be important in supporting diurnal and seasonal transpiration of woody plants. In special situations, it has been observed that internal storage can provide a significant proportion of the total diurnal and even seasonal water use by a plant (e.g., Čermák et al. 1982, 1984, Goldstein et al. 1984, 1998, Borchert 1994). If storage is minimal in large trees, then water loss would either result in severe water deficits or prolonged stomatal closure. Either of these outcomes would have consequences for growth and survival. Therefore, we contend, as suggested by older work with trees, that stored water plays a biologically significant role.

Water transport in large old-growth trees occurs over long distances via conducting elements that may have low hydraulic conductivities (Gartner 1995, Sperry 1995, Ryan and Yoder 1996). Even in short-stemmed woody plants, there may be a

considerable delay between water loss from the foliage and water uptake by the roots. For example, Hellkvist et al. (1974) noted a 6-hour difference between the drop in foliage water potential and a drop in root water potential in relatively young *Picea sitchensis* (Bong.) Carr. trees.

A study of the water relations of large old-growth trees at the Wind River Canopy Crane Research facility has enabled us to re-examine the topic of stored water. The presence of a tall Liebherr high-rise construction crane (top of mast 87 m) provided access to about 2.3 ha under the 75 m jib. During the summer of 1996, we measured foliar water potential, stem water content, stem and branch sap flux and stem dimensional changes in a 57-m tall Douglas-fir tree, one of the tallest single trees ever equipped with instruments to monitor in vivo water flux dynamics. (Much taller trees have since been studied; e.g., Koch et al. 2004.) Measurements were taken at multiple heights and positions. Additional, but spatially limited, measurements of stem sap flux and stem water content were made on two other Douglas-fir trees.

Materials and methods

Study site and study trees

The Wind River Canopy Crane Research site is located near the Columbia River in Washington. Details about its location, soil and climate have been described elsewhere (Shaw et al. 2004).

Three dominant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; hereafter Psme) trees were sampled for stem tissue water content and one Douglas-fir, Psme 1373, was selected for intensive short-term study of tree water storage based on branch and stem sap fluxes, twig water potential and stem dendrometer measurements. Detailed biometric and physiological measurements were made on Psme 1373, and supplemental measurements were made on the other study trees to validate absolute values and patterns. The sample trees were between 450 and 480-years-old, their heights were in the upper 20% of trees in the crane circle. Psme 1373 was 1.29 m in diameter, 57 m tall and had a live crown length of 31 m and a projected crown area of 95 m^2. Sampling heights were partially dictated by the presence of the Rose Canopy Platform at 46 m and a 4.5 m mountaineering ladder above the platform. Additional information about Psme 1373 has been presented by Bauerle et al. (1999).

Sap flow measurement and calculation

Six stem sap-flow, six branch sap-flow and two dendrometer sensors were installed on Psme 1373. The sensors were positioned to capture the vertical and circumferential variation in sap flow and the vertical variation in dimensional changes in elastic stem tissues. Two sensors on opposite crown sides (South, North) were placed on branches at heights of 46, 51 and 56 m, four sap flow sensors were installed near the stem base at a height of 4 m (from cardinal points) and two in the upper stem at 51 m (again on opposite stem sides; see Figure 1). Sap flow in the main stem was measured by a stem heat balance (THB) method applied to a stem section with internal (direct electric) heating of tissues (Čermák et al. 1973, 1982, 2004, Kučera et al. 1977, Tatarinov et al. 2005). The method used five stainless steel 25 × 1 mm rectangular electrodes that were inserted in parallel at 20 mm distances into the sapwood to the depth of the sapwood–heartwood boundary. A compensating system of eight thermocouples (Cu-Cst) was used (Čermák and Kučera 1981) with two EMS P-2 sap flow meters producing constant power (1 W) and data loggers (Environmental Measuring Systems, Brno, Czech Republic). Sensors were insulated with 2-cm-thick open-porous polyurethane foam, shielded from radiation by aluminum foil, and protected from rain by a polyethylene sheet fastened to stem surface with sealing wax. Because the upper stems of the old-growth Douglas-fir trees in this forest are exposed to high radiation loads, the stem immediately above and below the two sets of sensors in the upper part of Psme 1373 was shielded with a 2-m-long section of aluminum foil. Sap flow in six branches was measured by a method similar to that for the main stem, but applying EMS Baby-1 sensors with flexible external heating and sensing (based on Čermák et al. 1984, 2004 and Lindroth et al. 1995). Study branches were at tips of healthy, full-sized branches. Branch tips averaged 13.4 mm in diameter and carried ~100 g_{DW} of needles (~0.37 m^2 of foliage). Branch sensors were insulated with foam and shielded with a silver-coated mylar sheath. The ends of the mylar sheaths were fastened to the smooth bark surface with polyethylene tape. Both variants of the THB method measure total sap flow within selected stem sections delimited by electrodes (integrating the radial pattern of flow by combination of two thermocouples placed at different depths and bulk heating of tissues) or in branches, where circumferential heating was applied (Čermák et al. 2004, Tatarinov et al. 2005 and literature cited therein).

The diurnal course of sap flow within the stem (Q_t) was compared with that of branches (q_{br}) located above that point. Branch sap flow (g m_{sw}^{-2} h^{-1} on a sapwood area basis) in each crown section was assumed to be the mean of sap flow in the branches (q_{sh_mean}; g m_{sw}^{-2} h^{-1}) at the top and bottom of that crown section and converted to a leaf area basis q_{sh_mean} (g m_{leaf}^{-2} h^{-1}):

$$q_{br\_mean} = \left(\frac{q_{br\_bottom} + q_{br\_top}}{2} \right) \quad (1)$$

where q_{br_bottom} is the mean sap flow of the two branch sensors at the bottom of the crown section under consideration and q_{br_top} is the mean of the two branch sensors at the top.

Because branch sap flow was not measured below 46 m, we assumed that branch sap flow measured at 46 m would decay in a linear fashion and approach zero at the base of the live crown (26 m). Previous studies comparing sap fluxes from the largest to the smallest tree in a stand (e.g., Čermák and Kučera 1990, Martin et al. 1997, 2001, Tatarinov et al. 2000) and those studies comparing branches within the crown of a single tree (e.g., Hinckley et al. 1994) support this assumption. Sap flow

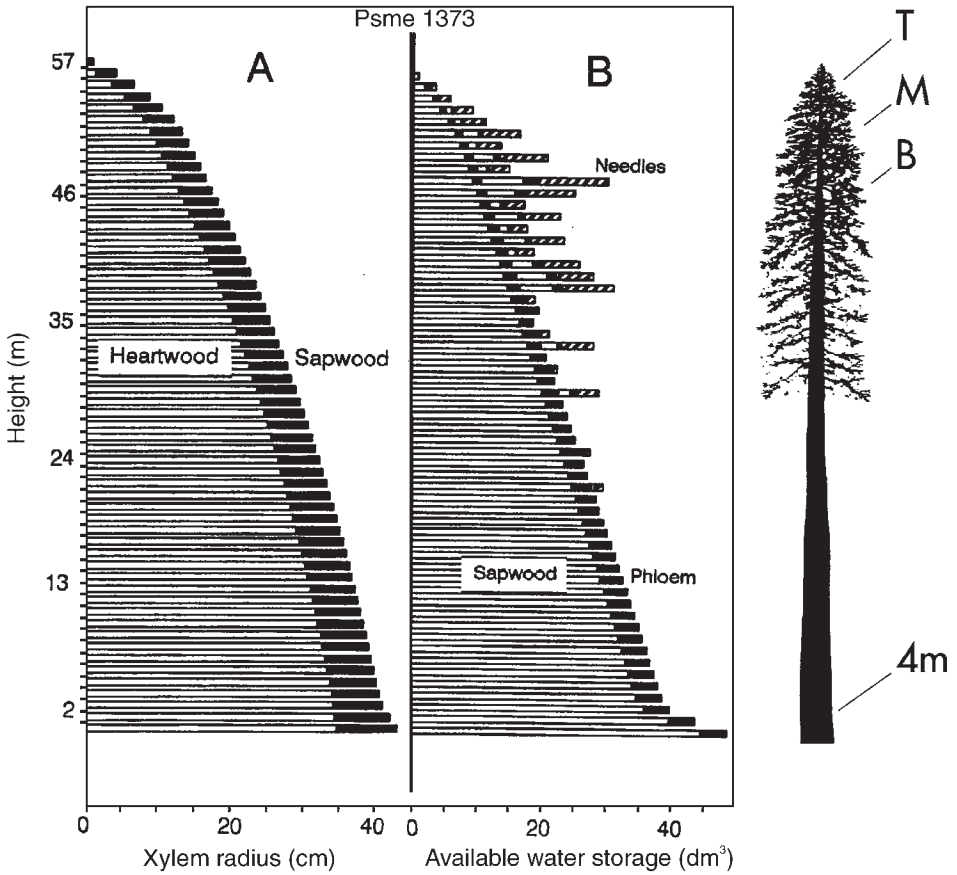

Figure 1. Sample tree (right) showing the positions of sap flow sensors at heights of 4, 46 (B), 51 (M) and 56 m (T). Vertical pattern of stem form (A; delimiting sapwood and heartwood) and free water content in the sapwood, phloem and needles (B) in the old-growth Douglas-fir sample tree (Psme 1373). Horizontal bars represent 1-m thick layers above ground, including tree stem, branches and needles.

in the stem cylinder between 4 and 51 m (Q_{t_med}; $kg_{stem}\ h^{-1}$) was derived as the difference between the inflow (Q_{t_4m}) into, and outflow (Q_{t_51m}) from, this section:

$$Q_{t\_med} = Q_{t\_4m} - Q_{t\_51m} \quad (2)$$

where Q_{t_4m} is assumed daily total tree water use. Similar calculations were made for branches:

$$Q_{crown\_med} = Q_{crown\_tot} - Q_{crown\_top} \quad (3)$$

where Q_{crown_med} is sap flow for the mid-crown, Q_{crown_tot} is sap flow for the whole crown (equal to that for the whole tree) and Q_{crown_top} is sap flow measured just below the top.

Estimation of water storage and tissue volume

We estimated wood and foliage water storage gravimetrically (biometric samples), hydrometrically (based on sap flow) and volumetrically (with dendrometers). For some of the water content estimates, it was necessary to determine bole, branch and foliage volumes. Total volumes of aboveground tree tissues including the stem and foliage were estimated biometrically. Volumes of stem xylem, phloem and bark, and branch xylem, phloem and bark, were estimated from diameters and cores taken at stem heights of 4, 46 and 51 m.

Foliage volume was calculated from (1) measurements of height above ground, diameter, length and foliage volume of all live branches (Ishii et al. 2002) and (2) estimated foliage quantity based on sapwood basal area and branch size and position. Sapwood cross-sectional area at any height on the bole of a Douglas-fir is related linearly to the amount of foliage above that point (Long et al. 1981). In addition, our two estimates of foliage quantity were compared with a third estimate derived from sapwood cross-sectional area at 4 m (McDowell et al. 2002).

The longitudinal or vertical section of the stem in Figure 1 was reconstructed from the sapwood cross-sectional area using a tree stem form factor (Korf et al. 1972, Philip 1994) with total stem volume converted to sapwood and phloem volumes. Free water volume in the sapwood (V_{w_free}/V, expressed as a percentage of total sapwood fresh volume, V) was calculated by subtracting the volume of water in the heartwood (V_{w_htrw}, taken as mostly physically bound) from that in the sapwood (V_{w_sapw}) (Zimmermann and Brown 1971, Kravka and Čermák 1995):

$$\frac{V_{w\_free}}{V} = \frac{V_{w\_sapw}}{V} - \frac{V_{w\_htrw}}{V} \quad (4)$$

Changes in stem radius of Psme 1373 at heights of 4 and 46 m were measured with a temperature compensated electronic radial dendrometer (DR-01, EMS Brno, Czech Repub-

lic). A steel radial rod was inserted through a 7-mm diameter hole (which extended 80 mm through the sapwood and was a little wider than the rod so that the rod was not touching the sapwood) and screwed tightly into the heartwood. A magnetic sensor (Diana Inc., U.K.), whose sensitive point was in direct contact with a smooth bark surface (located 5 cm below the rod), was fastened to the rod; its temperature was measured with an attached platinum thermometer. The bark was removed and smoothed to a distance about 1 mm from the bark cambium and phloem. The dendrometers were insulated and shielded as described for the sap flow sensors.

Gravimetric water storage estimates

Stem tissue water content was estimated by classical methods. Bark, phloem, and xylem radial water contents (% of volume) were measured gravimetrically on 5.2-mm diameter cores taken with an increment corer (Suunto, Finland). Immediately after sampling, each core was protected by tightly wrapping it in aluminum foil and stored in a shielded polyethylene bag. Within 24 h, each core was cut into short pieces of known length; these were individually marked, weighed, oven-dried at 90 °C for 24 h and re-weighed. The specific mass of xylem dry matter was assumed to be 1.54 g cm^{-1} and volume was attributed to three fractions: dry matter, water and air (Kravka and Čermák 1995). The phloem was assumed to contain the same fraction of free water as the xylem sapwood. The amount of free stored water was calculated by multiplying the volume of a particular tissue by the volumetric percentage of free water. We defined free water as the amount of water measured in the sapwood after subtracting the amount of water measured in the heartwood.

Needle water content was measured at 55.9, 51.1, 44.2, 39.1 and 26.4 m in current-year, 1- and 2-year old foliage sampled from the south side of the crown. Needle free water was estimated based on percent water content values obtained from small samples multiplied by the quantity of foliage in 1-m zones. Samples were taken in late October when tissues were well hydrated. Needles were oven-dried at 65 °C for 72 h. The foliage area, mass and volume in these zones were estimated knowing total foliage parameters (from sapwood area) and its distribution along the stem (derived from the distribution of branch foliage volumes).

Hydrodynamic water storage estimates (sap flow)

For Psme 1373, we had estimates of the total foliage and its vertical distribution and the amount of water lost from six branches (q_{br}). When q_{br_mean} (kg m_{leaf}^{-2} h^{-1}) for each crown section was multiplied by the leaf area for that section and then summed to give Q_{crown} (kg h^{-1}), Q_{crown} overestimated Q_t, because branch sap flows were measured in branches at the outer, more exposed edges of the crown, which overestimated water loss for that section. To correct this error, q_{br_mean} was converted to total sap flow for each section of the crown by using apparent leaf area A_{app} (m^2 $part^{-1}$) and the formula:

$$Q_{crown} = q_{br\_mean} A_{app} \quad (5)$$

where A_{app} was determined in an iterative process so that Q_{crown} equaled Q_t for each day (assuming that there were no water losses from a stem without foliage). Daily total Q_{crown} was first calculated by multiplying q_{br_mean} by leaf area (A_{actual}) and this value was compared with the daily summed Q_t derived from sap flow data. Actual leaf area was reduced and Q_{crown} was recalculated. The process was continued until Q_{crown} matched Q_t for that day. At that point, A_{app} for the tree crown was known.

The change in stored water (ΔQ; dm^3) at any time in the whole tree (or in a specified part of the tree) became discernible when the difference in sap flow between the stem and small branches was calculated:

$$\text{Cum } \Delta Q = \sum_{t}^{t+1} (Q_{branch} - Q_{stem}) \Delta t \quad (6)$$

where Δt is the time step and can range from the length of time between data logging to the entire day. Negative values of ΔQ occur between sunrise and early to mid-afternoon and represent times when water stores are being depleted. Positive values of ΔQ indicate refilling of depleted water storage tissue, which occurs from mid-afternoon to well into the evening or until the next dawn.

Because the daily totals of flow, Q_{crown} and Q_t, were equal (only small differences can be expected between consecutive days), data collected over short periods within a day can be compared to estimate the amount of water extracted from tree storage during a particular day (W_{stor}):

$$W_{stor} = (\pm)\ \Delta Q = Q_t - Q_{crown} \quad (7)$$

where, for each recorded time step (1 or 15 min) during a diurnal course, a series of differences, $+\Delta Q$ and $-\Delta Q$ resulted. Their summation for the morning hours provided an estimate of the use of stored water ($-\Delta Q$), whereas their summation in the late afternoon and evening hours ($+\Delta Q$) gave an estimate of the refilling of stored reserves.

Volumetric water storage estimates (dendrometers)

The diurnal curve of cumulated ΔQ should reflect changes in tissue water content and thus should be comparable with diurnal changes in the volume of extensible tissue (e.g., sapwood, phloem and a negligible part of cork bark (see Molz and Klepper 1973, Hinckley and Bruckerhoff 1975)), measured as ΔR with dendrometers in addition to water changes in inelastic tissue (e.g., cavitation). This comparison can be made only when ΔQ and ΔR are expressed in comparable units. First, recorded data changes in stem radius (ΔR based on an initial radius, R_{orig}) were converted to changes in stem cross-sectional area (ΔA). These changes were expressed on a volume basis, ΔV, by multiplying the length (L) of the corresponding stem segment, L_i (or lengths of upper, middle and lower part of the stem) by a stem form parameter (f):

$$\Delta V_i = \{\pi[(R_{orig\_i}+\Delta R)^2 - R_{orig\_i}^2]\}L_i f \quad (8)$$

Then ΔV_i values for a particular stem segment were compared with the ΔQ_i for that segment.

Water potential measurements

After foliage expansion was complete, water potential and transpiration values were obtained during summer 1996 from two branchlets of each of the study trees (heights ranged from 56 to 65 m) with a pressure chamber (Soil Moisture, Santa Barbara, CA) and an LI-1600 porometer (Li-Cor, Lincoln, NE). Measurements were taken at predawn and solar noon in both aluminum-foil-covered and uncovered branchlets and then soil-to-leaf hydraulic resistance was calculated by the Ohm's Law analog. The study trees had statistically identical values at predawn and solar noon once height was accounted for. Details are provided in Bauerle et al. (1999). Three specific hydraulic resistances were calculated and then compared. First, water potential values taken at solar noon in uncovered branches were plotted against the corresponding transpiration rate—the slope of this line is the hydraulic resistance to water flow and provides an estimate of resistance between roots and foliage (i.e., a long-distance resistance, see Elfving et al. 1972, Camancho et al. 1974). Second, water potential values taken at solar noon in covered branches were plotted against the transpiration rate measured in the paired uncovered branch (i.e., a short-distance resistance, see Brooks et al. 2003). Third, leaf specific conductivity (LSC or 1/resistance) was calculated for August 29, with a sap flux density of 0.08 kg m^{-2} h^{-1} (at 56.7 m) as the estimate of transpiration rate for the upper crown and predawn and solar noon water potentials were corrected for the gravitation potential (to provide the water potential gradient). These values were compared against each other and against previously reported values.

Data collection and logging

The study began on July 24 and ended on October 15, 1996 (75 days in total). Data were measured every minute and stored as 15-min means over 2-week periods or every minute for 3-day periods. Data stored at minute intervals included the following measurements on Psme 1373: the N and S sap flow sensors at 4 m, all sap flow sensors at 51 m, and all branch sap flow sensors and both dendrometers (at 4 and 46 m). Data stored as 15-minute means were obtained from the stem sap flow sensors at 4 m on the E and W sides of Psme 1373.

Results

Stem tissue water content of sample trees

Evaluation of cores at the stem base (4 m, the tree had 250 mm thick bark at that height) showed that phloem and xylem dry matter (i.e., mainly cell walls) represented about 27%$_{vol}$ of total tissue volume of the Douglas-fir Psme 1373. The fraction of water was about 5%$_{vol}$ for the bark, about 10%$_{vol}$ for the heartwood, about 32%$_{vol}$ for the phloem and around 44%$_{vol}$ for the sapwood. Similar values were found in the other two sampled trees. Values at the mid-crown (46 m) were similar to those at the stem base except that heartwood water content was only about 6%$_{vol}$. The sapwood of Psme 1373 was about 5 to 8 cm deep (i.e., 13 to 20% of the xylem radius) at 4 m, and about 4 to 5 cm deep (18 to 27% of the xylem radius) at 46 m. When considering the whole tree (see Figure 1), the sapwood represented about one third of the total xylem volume (5363 versus 16,993 dm^3, i.e., about 56 mm when expressed on a crown projected area basis) and of that about one quarter was free water (or about 1217 dm^3 of water, i.e., about 13 mm). This volume of water represented the majority of total free water (85%) in the tree. The total amount of free water in the stem phloem of Psme was over 161 dm^3 (i.e., 11% of the total free water) and in the branch sapwood and phloem it exceeded 71 dm^3 (i.e., 5% of total tree water). The needle free water fraction was 47 dm^3 (or 3.3% of total tree water). When one considers the vertical distribution of free water in the upper crown (above 51 m), there was about 4 dm^3 in the stem phloem, 21 dm^3 in the stem sapwood, 8 dm^3 in the branch sapwood and phloem, and 7 dm^3 in the needles. Thus, free water in the treetop totaled 41 dm^3 and represented about 3% of the total free water in the tree. In contrast, 97% of the total free water in the tree was found below 51 m, with 6, 39 and 52% in the middle crown, lower crown and bare stem, respectively (Table 1).

Water storage and daily transpiration

Diurnal courses of sap flow over 10 days from late July to October (Figure 2 shows four days selected at roughly monthly intervals), as estimated by the heat balance method, illustrate the magnitude of the temporal variation in sap flow in the stem of Psme 1373 measured at 4 and 51 m. The measurements at 4 m height capture sap flow at the base of the tree and for the entire crown of the tree, whereas the measurements at a height of 51 m (i.e., upper crown) capture only the upper 6 m of the crown (representing 20% of this tree's crown length and carrying about 33% of the total foliage). Whole-tree transpiration during clear days ranged between 150 and 300 dm^3 day^{-1} over the study period (about 1.6 to 3.2 mm day^{-1} when expressed on a crown projected area basis). Phillips et al. (2003) found that maximum daily water use in a nearby, but larger and taller, Douglas-fir (~65 m) did not exceed 370 dm^3 day^{-1} on clear days.

For Psme 1373 for August 1 (Figure 3), Q_t (equal to Q_{crown}) was 196 dm^3 (i.e., the integrated value under "crown total"; or under "stem total"). Upper crown and stem sap flow on the same day above 51 m was 128 dm^3, i.e., 65% of the total (= the highest seasonal value). When considering 10 clear days, the upper crown transpired on average 50 to 65% of the total tree water loss. Based on calculations of $Q_{lower\ crown}$ (= $Q_{crown\ total} - Q_{upper\ crown}$), water loss from the lower crown averaged 89 dm^3 day^{-1} (62 to 114) or 45% (36 to 55) of the total tree water loss. Expressed as flow density per leaf area, the values were 0.34 and 0.85 dm^3 m^{-2} day^{-1} for the whole tree and upper crown, respectively. Thus for clear days, water loss from the upper crown (or stem) was almost equal to water loss from the rest of

Table 1. Volumes and amounts of free water in parts of the Douglas-fir sample tree, Psme 1373.

	Volume (dm^3)					Free water (dm^3)				
	Upper crown > 51m	Mid-crown 46–51m	Lower crown 23–46m	Bare stem < 23m	Tree total	Upper crown > 51m	Mid-crown 46–51m	Lower crown 23–46m	Bare stem < 23m	Tree total
Stem sapwood	92	186	1931	2912	5122 = 81.0%	21	42	438	661	1163 = 81.6%
Stem phloem	13	21	204	316	554 = 8.8%	4	7	58	76	145 = 10.2%
Stem sapw + phl	105	207	2135	3229	5676 = 89.7%	25	49	497	737	1308 = 91.8%
Branch sapwood	29	77	135	0	242 = 3.8%	7	17	31	0	55 = 3.8%
Branch phloem	6	16	29	0	51 = 0.8%	2	5	9	0	16 = 1.1%
Branch sapw + phl	35	93	164	0	293 = 4.6%	8	23	40	0	71 = 5.0%
Sapwood total	121	263	2067	2912	5363 = 84.8%	28	60	469	661	1217 = 85.4%
Phloem total	19	38	233	316	606 = 9.6%	6	12	67	76	161 = 11.3%
Sapwood + phl total	140	301	2299	3229	5969 = 94.4%	34	71	536	737	1379 = 96.7%
Needles total	54	105	198	****	357 = 5.6%	7	14	26	****	47 = 3.3%
Wet tissues total	194	405	2497	3229	6326 = 100%	41	86	562	737	1426 = 100%
	3.1%	6.4%	39.5%	51.0%	****	2.9%	6.0%	39.4%	51.7%	****
Stem total	237	608	5948	10200	16993 = 100%	****	****	*****	*****	****
	1.4%	3.6%	35.0%	60.0%	****	****	****	*****	*****	****

the tree below and seemed more stable than water loss from the lower crown. In addition, the uppermost foliage always transpired disproportionately more water (> 2.5× in relation to needle area) than that of the middle and lower crown. Similar results were noted by Čermák and Kučera (1990) in large Norway spruce trees.

Diurnal course and time lag

The diurnal course of sap flow closely followed foliar transpiration and thus started first in branch tips, then in branches, somewhat later in the stem near branches and with the most pronounced delay in the stem furthest from the foliage. The top 6 m of the crown and the whole crown appear to begin transpiring almost at the same time; integrated sap flow in branches of the upper crown showed no significant time shift compared with the crown total (see Figure 3; maximum lag was less than 15 min), or with stem sap flow at 51 m. In contrast, a pronounced time shift was noted between stem sap flow at 51 m and at 4 m. Sap flow at the stem base lagged that of the whole crown by 1 to 2 h. The time lags were even more pronounced after sunset. Transpiration from the upper crown or total crown ceased about 2030 h, almost 4 h before sap flow approached zero at 51 m and 4.5 h before it approached zero at 4 m. During the morning hours, the water balance of the tree stem between 4 and 51 m was negative. For about 2 h, outflow to the upper stem was greater than inflow from the lowermost stem (below 4m). The balance became positive again at about 1000 h when input into the stem at 4 m was greater than output at 51 m. Depleted water storage was recharged in the afternoon and at night until the early morning hours of the next day when transpiration resumed.

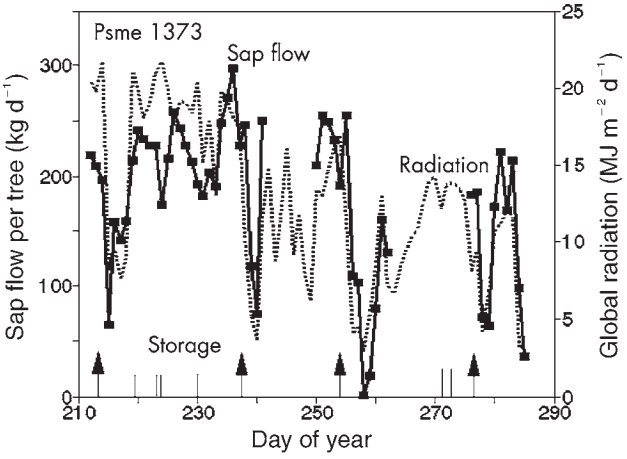

Figure 2. Seasonal course of daily sap flow in the old-growth Douglas-fir sample tree (Psme 1373) and daily global radiation in the Wind River experimental plot. Short lines indicate 10 individual days with fine weather selected for detailed analysis of water storage, arrows indicate days shown in following figures.

Similar to the timing of sap flow lags, temporal variation in sap flow decreased from the individual branch to the whole crown (data not shown) and from the upper stem to the lower stem. Sap flow variation was higher in small, foliated branches and decreased in the main stem with increasing distance from the foliage. As the distance from the transpiring surface increased, more transpiring surfaces were integrated and more tissue buffering capacity was involved, thus the diurnal curves in the lower stem appeared quite smooth (see Figure 3).

Diurnal courses of sap flow and changes of stored water

Diurnal changes in water storage were varied over the growing season, but had the same general pattern. Stored water was de-

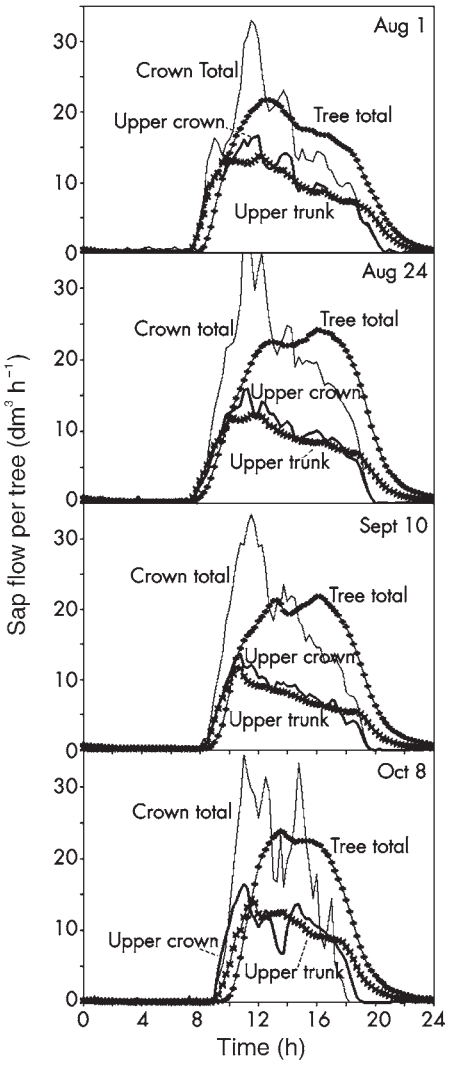

Figure 3. Diurnal measures of sap flow in the old-growth Douglas-fir sample tree (Psme 1373) at the base of the stem and for the upper crown on four selected days with fine weather (August 1 and 24, September 10, October 8). Crown totals represent sap flow measured in branches distributed at six locations in the crown. Stem totals represent flow measured at the stem base (at a height of 4 m). Upper crown represent flows measured in branches close to the tree top (above 51 m), upper stem represents flow measured in the stem at the height of 51 m.

pleted mostly during morning hours and replenished during the afternoon, particular changes were dependent on weather conditions.

On a daily basis, water withdrawn from storage equaled water returned to storage (consequently $Q_t = Q_{crown}$, which fits for day-to-day changes, but not for a growing season). The results presented in Figure 3 illustrate the within-day behavior of stored water, whereas data in Figure 4 represent the total water used from storage. The mean daily total quantity of water withdrawn from storage for the whole tree Psme 1373 was about 45 dm^3 (varying between 34 and 53 dm^3) and for its upper crown it was about 13 dm^3 (9–27 dm^3). The relative quantity of stored water used from the whole tree was appreciable and represented about 23% (20–31%) of daily total sap flow, compared with only about 7% (5–16%) of daily sap flow used from the upper crown. When expressed as a percentage of total free water, total stored water used on clear days was 3.0% (2.3–3.6%) and that from the upper crown was 0.9% (0.6–1.8%): therefore, it was a relatively small fraction of total free water, likely reflecting our definition of free water (see Figure 1). However, as a percentage of total water lost by transpiration, the daily use of stored water (~23%) represented a biologically significant quantity.

Water withdrawn from storage came from both the upper stem (> 51m) and the lower stem (< 51m); however, the quantity coming from the lower stem was 3 to 5 times that from the upper stem. Most of the stored water (75%) came from the zone between 4 and 51 m (see Figure 3 and 4). The volume of free water in the tree was an order of magnitude larger below 46 m than above 46 m (Table 1). For the upper part of the tree (i.e., above 51 m), water used from storage was about 10 dm^3. Both elastic (phloem, needle, etc.) and inelastic tissue volumes were small in the top of the tree (see Figure 1) and between 38 and 65% of these volumes could be withdrawn. There was considerable temporal variability in water removed from or returned to storage in the upper part of Psme 1373 (Figure 4).

Although there was a net depletion of water from storage in the morning and early afternoon, there were short periods of recharge. The pattern for the tree below 51 m was easily divided into distinct phases of depletion and recovery (Figure 4). As shown in Table 1, the amount of free water in the upper stem was considerably less than in the lower stem (140 versus 5969 dm^3, or 2.3% of the total). Thus, the percentages of free water observed in the two regions differed (~24 versus ~4% for the upper stem and whole tree, respectively) even though the absolute amounts were in the opposite direction (~10 versus ~50 dm^3, respectively; see Figure 4). From the standpoint of proximity (when compared with soil water) and volume, the sapwood of the lower stem was most important. This was evident in the distribution of free water in different tissues (stem sapwood and phloem, branch sapwood and phloem and needles) and at different heights (upper middle and lower crown and bare stem below crown; see Figure 1).

Diurnal changes in stem volume and stored water

The radius of the stem (R) measured at 4 and 46 m changed appreciably during a 24-h period (Figures 5 and 6). Values of ΔR reported in this study (with observed daily amplitude of about 0.1 mm) largely reflect volumetric changes in elastic tissues and associated changes in their water content as first suggested by MacDougal (1925), Arcikhovskiy (1931), and Molz and Klepper (1973). The maximum radius was noted between 0730 and 0800 h at both 4 and 46 m. At 46 m, a minimum occurred around 1400 h; there were no further changes in stem radius until 1900 h, when radius increased rapidly. In contrast, stem radius was minimal at 1730 h at 4 m. Stem radius continued to increase through the night, but at a lower rate. The steeper slope during recovery at night likely illustrates rehy-

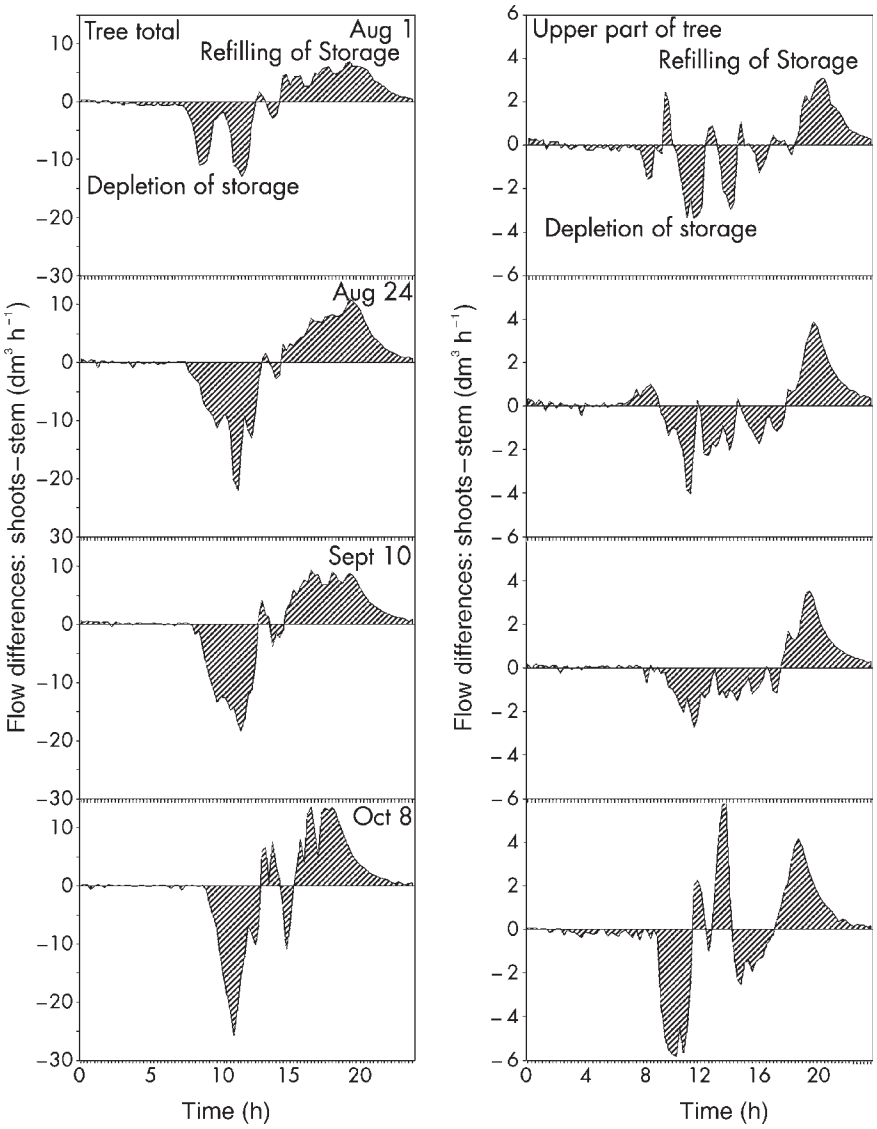

Figure 4. Diurnal courses of differences between transpiration of crown foliage (sap flow in branches) and sap flow in the stem for the whole tree (whole crown and stem base; left) and upper crown (above height of 51m; right) in the old-growth Douglas-fir sample tree (Psme 1373) for four selected days with fine weather (August 1 and 24, September 10 and October 8).

dration, whereas the gentler slope late at night and early in the morning suggests growth. Diurnal changes in stem volume paralleled the cumulated difference in sap flows during daytime and volume increases during night, when no storage water is extracted from tissues. The time shift, however, was larger for the whole tree than for the upper crown.

The slightly greater dimensional changes in the upper stem radius than in the lower stem radius confirmed earlier findings of Dobbs and Scott (1971). For Psme 1373, the diurnal pattern of stem shrinkage ($-\Delta R$ and ΔQ), refilling ($+\Delta R$ and $+\Delta Q$) and growth ($+\Delta R$) was similar at the base of the stem to that in the upper crown. However, there were large differences in the timing of changes in stem volume and water storage in the upper stem versus the lower stem, 15 min versus 3 h (Figure 6). The delay in the upper stem increased substantially during the growing season, whereas the delay in the lower stem remained constant. If these time shifts are taken into account and the late night and early morning increases due to growth are excluded, then the relationship between a volume change and a change in water storage was linear during most of the daytime—from about 0800 to 2100 h (Figure 7).

Diurnal changes in stem volume (ΔV calculated from measured ΔR with Equation 7, Figure 6) were strongly related to changes in the quantity of water removed from storage ($\pm \Delta Q$) (cf. Figures 6 and 7). Stem volume decreased with increasing transpiration (and water depletion from storage, $-\Delta Q$) early in the day and increased with decreasing transpiration (and gradual refilling of storage, $+\Delta Q$) later in the day. Despite these changes, growth or a net day-to-day increase in volume occurred only during the night when transpiration approached zero and internal storage comparments had been largely refilled.

When measured volume changes were expressed as fractions of free water for different tissues, they appeared highest for needles of the whole crown, followed by phloem and other wet tissues. The situation was similar when daily storage was evaluated the same way, but the significantly higher percentage volume change occurring in the upper crown indicated

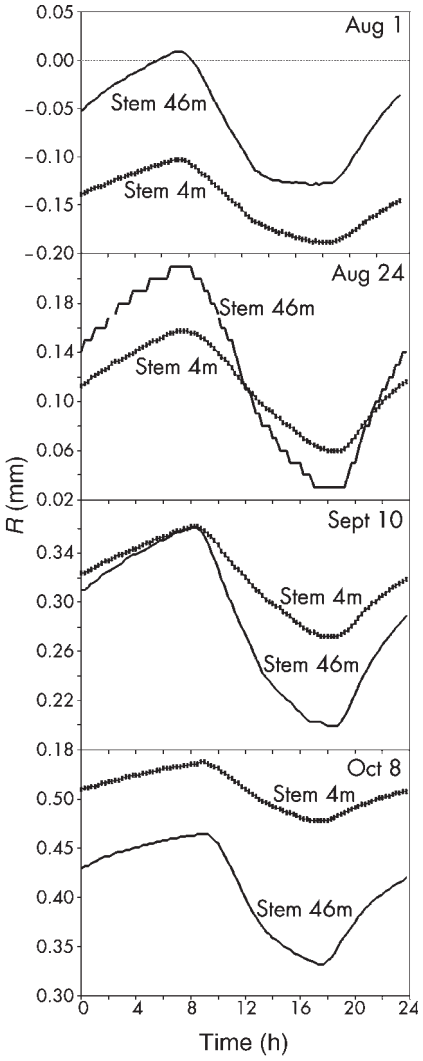

Figure 5. Diurnal measures of stem radius (R) at the height of 4 m (left) and 46 m (right) in the old-growth Douglas-fir sample tree (Psme 1373) during selected days with fine weather (August 1 and 24, September 10 and October 8). The radius displayed is real, but is relative to the measuring device—the actual radius would include the distance from the center of the stem to the measuring point (from the position at 4 m, this was about 500 mm).

higher tensions there (Figure 8). Changes in stem volume are caused by transpirational extraction of water from tissues and when taking into account the time shift (larger but almost constant for the whole tree, smaller but gradually increasing in the upper crown) both processes are linearly related. Soft tissues account for only a small proportion of stored water, most of which is in the sapwood.

Seasonal changes in daily water storage and stem volume

The amount of water withdrawn from storage on clear days was either relatively stable (upper crown and stem; Figure 8A: open rectangles) or increased as the season progressed (whole tree; Figure 8A: solid rectangles). For the whole tree, the amount of water withdrawn from storage each day increased from about 40 dm^3 in early August to 50 dm^3 in late September and ranged from 20 to 30% of daily sap flow. For the upper stem, water withdrawn from storage (~10 dm^3 day^{-1}) averaged about 10% of the water lost from the upper stem (96 to 128 dm^3; Figure 8B) and was relatively stable. The amount of water withdrawn daily from the whole stem represented 2 to 5% of the free stored water (again increasing from August to October). For the same period, but considering only the upper part of the stem, 20 to 25% of free water was used during the day (Figure 8C). There was a disproportionate use of stored water from the top of the tree.

Earlier in the season when about 40 dm^3 of stored water was used by the entire tree (Figure 8A), about 6 dm^3 came from changes in elastic tissues or about 15% of the total. This percentage decreased over the season. Daily volume changes in elastic tissues (averaged 6 and 0.4 dm^3 day^{-1} for the whole tree and upper crown, respectively; Table 2) were small compared with the total quantity of free water used from storage. If expressed as a percentage of free water, diurnal water used from elastic tissues of the entire tree never exceeded 0.5%. For the upper stem, it increased from 0.7 to 1.0% over the study period. Water from elastic tissue was never a substantial percentage of the total, about 14% of daily water used for transpiration derived from storage or about 1% of the free water. On average about 45 and 10 liters (about 23 and 10% of transpired water) were taken from storage when considering the whole tree and its upper part, respectively. This percentage did not change much for the whole tree during the study (it increased from about 20% in the fall to 31% in midsummer), but the percentage increased substantially in the upper part of the tree (the upper stem supplied twice as much in October, up to 27%, compared with earlier in the summer), even though tree water loss was about 33% lower at this time of the year.

Water turnover rate

When considering just free stored water from the upper crown and from the whole tree and their corresponding sap flows, stored water could meet transpirational needs for a little more than a third of a day (0.32 to 0.42) and for about a week (6.3 to 8.4), respectively (Table 3), with no clear seasonal variation.

Transpiration and water potential relationship

Figure 9 illustrates a constant decline in water potential as transpiration increased at the tops of the three study trees. The two slopes, short- and long-distance hydraulic conductivity, were similar and linear. The water potential difference between the two lines at a given transpiration rate corresponds to the frictional potential. Frictional potential is another negative constraint, in addition to the gravitational potential, that can decrease leaf water potential in these tall trees.

Discussion

Tree water storage in stems and branches

Sapwood and heartwood water contents at the stem base of the studied trees were similar to those observed in other conifer-

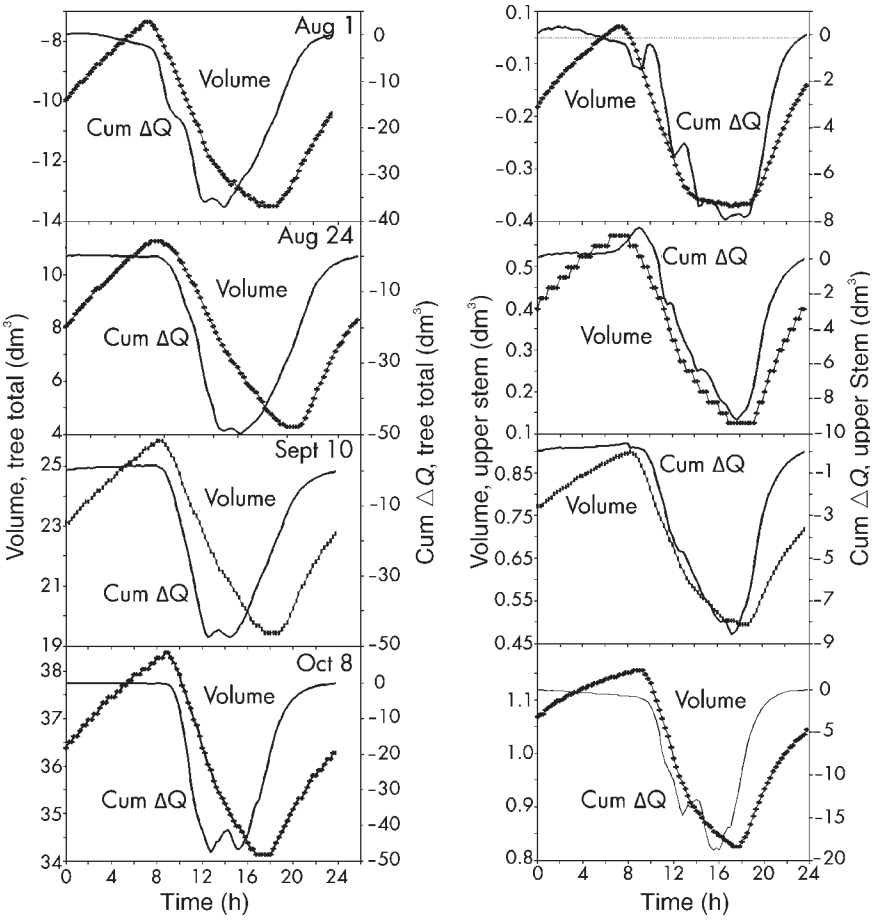

Figure 6. The change in stored water at any time (Cum Δ*Q*) and stem volume (*V*) calculated for the whole tree (left) and for the upper crown (above 51 m; right) in the old-growth Douglas-fir sample tree (Psme 1373) during selected days with fine weather (August 1 and 24, September 10 and October 8). Scales differ because of the large range of values.

ous trees (Waring and Running 1978, Sellin 1991*b*, Čermák and Nadezhdina 1998, Kravka et al. 1999), which also fit for needle water content (Čermák et al. 1983). The extremely low heartwood water content in the upper stem (46 m) of Psme 1373 was probably indicative of long-term desiccation. Unfortunately, additional and more extensive sampling was not permitted at the protected site.

Based on tissue volumes, water contents and assumptions about free water as a proportion of total water, we estimated that Psme 1373 contained 1426 dm^3 of free water (Table 1). Most of this water was in the stem sapwood below a height of 46 m and represented the greatest source of stored water used daily in transpiration. Water stored in tissues above 46 m and in elastic tissues was also used, but these sources were less important. Similar results were noted by Phillips (unpublished data) for a nearby 65-m-tall Douglas-fir tree. In contrast, water storage in the upper half of the stem of *Pinus pinaster* Ait. was reported to be more significant than in the lower portion of the stem (Loustau et al. 1996); however, the pine trees studied by Loustau et al. (1996) were considerably smaller than Psme 1373.

Water can be stored extracellularly or intracellularly in plant tissues (Arcikhovskiy 1931, Holbrook 1995). In contrast to extracellular stem water, intracellular water in trees is mostly confined to living tissues between the bark and the newly derived xylem. These tissues are highly elastic and may undergo considerable dimensional changes during the day (Dobbs and Scott 1971, Klepper et al. 1971, Goldstein et al. 1984, Milne 1989, Franco-Vizcaino et al. 1990, Holbrook and Sinclair 1992*a*, 1992*b*). For this large tree (Psme 1373), these intracellular stores represent less than 1% of daily water use. Extracellular water storage can be substantial in trees (Waring and Running 1978, Kravka et al. 1999) and involves water held by capillary forces in the sapwood as well as water released as a result of cavitation (Zimmermann 1983, Tyree and Yang 1990). Easily available ("free") extracellular or capillary water could represent a substantial fraction of water (Holbrook 1995). Under severe drought, water released by cavitation may support survival by preventing desiccation of fast-growing tissues (Dixon et al. 1984). Tyree and Yang (1990) concluded that water stored by small trees is mainly capillary water or water released by cavitation and may comprise a large volume; however, they also stated that the stored water in small trees is typically released at either very high or very low water potentials and thus has no significant role under most conditions, although Zweifel et al (2001) reported that sap flow is buffered by storage in small trees.

Our results for the large Psme 1373 tree suggest otherwise. As water is transpired from the foliage, water is withdrawn from needle tissue reserves (small), tensions develop in the

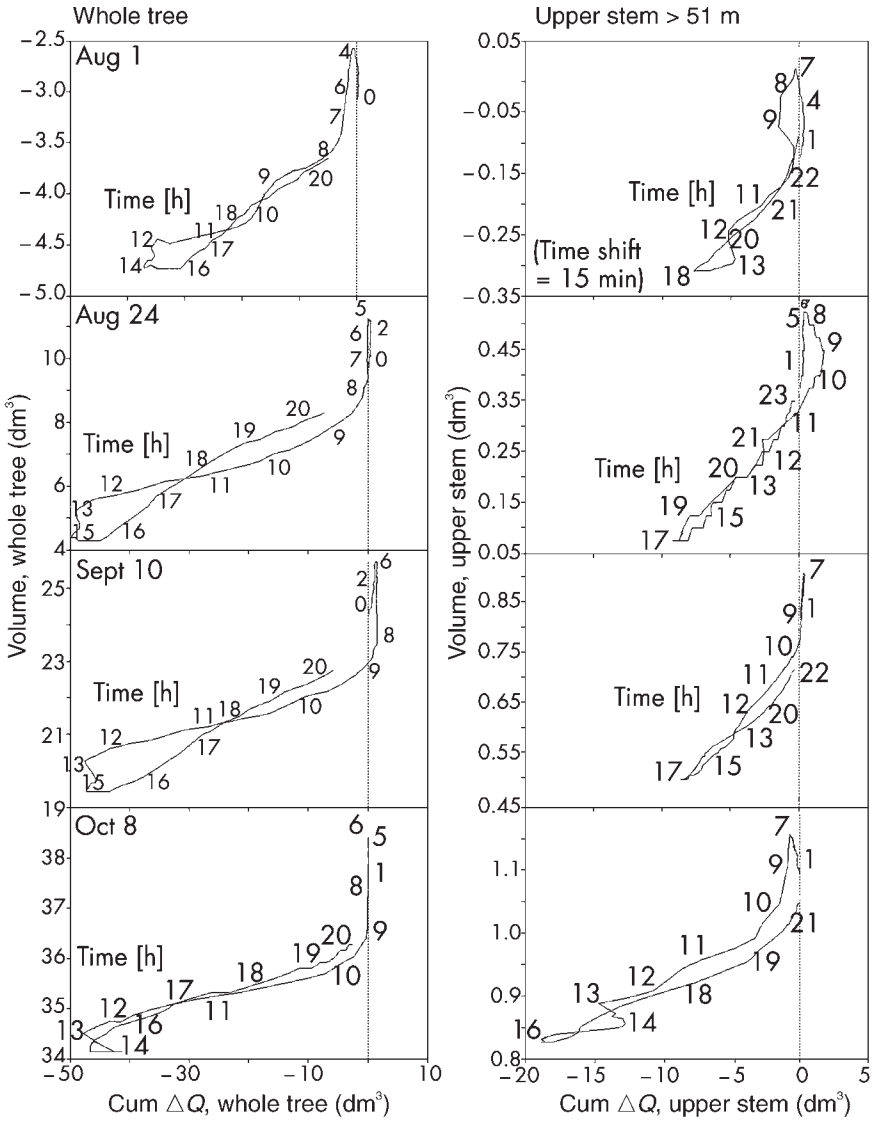

Figure 7. Relationships between the change in stored water at any time (Cum ΔQ) and stem volume (indicative of a volume of water), calculated for the whole tree (left) and upper crown (right) in the old-growth Douglas-fir sample tree (Psme 1373) during selected days with fine weather (August 1 and 24, September 10 and October 8, see Figures 5 and 6). The originally curvilinear relationships became almost linear when considering time shifts amounting to about 3 hours at the stem base, constant over the growing season, but increasing from 15 minutes (midsummer) to 1.5 hours (fall) at the upper crown.

vascular tissue (e.g., Bauerle et al. 1999 for Psme 1373) and water may then be withdrawn from the xylem and phloem. The data presented in Table 1 and Figure 4 demonstrate that there was a large quantity of free stored water and most of this water was in the xylem sapwood below the most active portion of the crown. If these stores were biologically unimportant, there should be only small lags in sap flow between the branches and the upper set of stem sap flow measurement points (51 m) and from the upper stem to the lower stem (4 m). Our data, which are within the range described by other authors (Table 4), demonstrated large lags, especially during refilling. Recently, there have been several publications documenting the role of the stem as a usable reservoir of water (e.g., Perämäki et al. 2001, Sevanto et al. 2002, Meinzer et al. 2006). Considered alone, however, the treetop behaved like a small tree, showing minimal time lags and much less reliance on storage.

Tissue and whole-plant water relations

Three factors appear to influence the time lag between sap flow and transpiration. First, distance is important. Short distances between measurement points (e.g., the foliage at the tip of small twigs and the base of the twig) should result in relatively small lags. Second, the resistance to flow within the conducting elements is important: the smaller the diameter of the conducting elements, the greater the resistance. A conducting system containing cavitated elements would have an even greater resistance. According to electric circuit analogies of water flow through plant tissues, this resistance will have an effect on the characteristic response time and corresponding time lags of the tissue (Schulte 1993). Third, buffering capacity, or the quantity and availability of stored water, should exert an influence. For most plants, a combination of these factors affects the time lags observed. In 3-m-tall reeds (*Phragmites* spp.), Rychnovská et al. (1980) observed a lag between sap flow at the stem base and foliage transpiration in the order of minutes. In contrast, several other authors have noted much greater lags (tens of minutes to hours) for a variety of woody species (Morikawa 1974, Hinckley and Bruckerhoff 1975,

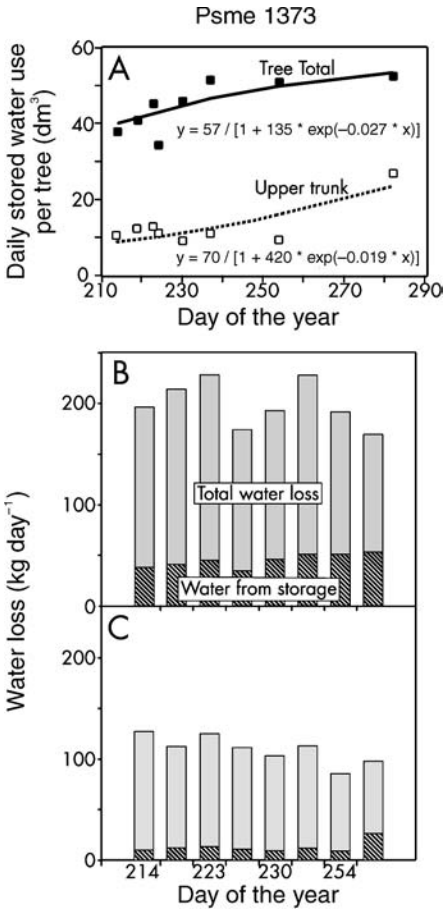

Figure 8. Daily water storage in the old-growth Douglas-fir tree (Psme 1373) during the growing season (A; values represent means for individual days), total daily water loss and fraction of that water taken from storage from the whole tree (B), and from the upper part of the tree (C).

Čermák et al. 1982, 1984, Schulze et al. 1985, Loustau et al. 1996, Phillips et al. 1996, Goldstein et al. 1998, Zweifel and Häsler 2001).

Diurnal courses of sap flow and changes of stored water

As first suggested by Ladefoged (1963), Morikawa (1974), Čermak et al. (1976) and Waring and Running (1978), large old-growth trees appear to have a large reservoir of water available on a daily or seasonal basis. Waring and Running (1978) estimated that the total storage capacity of any old-growth Douglas-fir forest is 267 m^3 of water per hectare (or 26.7 mm) and 75% of this water is stored in the stem sapwood. However, the data of Waring and Running have been criticized because they used a narrow-bore increment corer to collect samples (although the maximum error would likely be less than 10%; Morales et al. 2001). The absolute values of diurnal water depletion observed during the summer from our study of an old-growth Douglas-fir tree, 40 to 50 dm^3, appeared to match the estimates of Waring and Running and the measurements of Phillips et al. (2003) with an even larger,

Table 2. Mean daily water use and change in stem volume in a Douglas-fir tree, Psme 1373, in the whole tree and upper crown (51–57m).

	Upper crown	Tree total
Daily stored water use (dm^3)	10.9	50.4
Daily tissue volume change: (% vol)		
Sapwood	9.4	0.90
Phloem	191.2	31.3
Total	8.2	0.8
Daily stored water use relative to free water fraction: (% vol)		
Sapwood	41.6	4.1
Phloem	4.1	3.7
Total	23.1	3.4
Daily elastic tissue volume change (dm^3)	0.38	6.11
Daily elastic tissue volume change relative to: (% vol)		
Daily stored water use	3.5	0.81
Free water	13.0	0.41

nearby Douglas-fir tree (~ 65 m). However, our values generally exceed other published values (Čermák et al. 1976, 1982, 1984, Schulze et al. 1985, Goldstein et al. 1998, Kravka et al. 1999).

Our results suggest that the upper part of the stem is subject to much greater desiccation than the lower part. The upper canopy loses water more rapidly than the lower canopy because of the structure of this old-growth forest; the upper canopy is exposed to direct sunlight and is exposed to warmer, windier and drier conditions than the mid- and lower canopy. The upper canopy approaches the situation of a solitary tree (Čermák et al. 1984, Čermák and Kučera 1990, Parker 1997, Ishii et al. 2000, Ishii et al. 2002, Parker et al. 2002). Not only is the top of the tree exposed to drier conditions, but to a gravitational tension resulting in more negative water potentials, higher δC^{13} values, and lower stomatal conductances (Ryan and Yoder 1996, Bauerle et al. 1999, Woodruff et al. 2004). Greater use of free water and lower heartwood water contents all indicate greater desiccation, likely accounting for top dieback of many of the large Douglas-fir trees in the crane circle at the Wind River site.

Diurnal changes in stem volume and stored water

Diurnal changes in stem dimensions were thought to occur in tissues external to the rigid xylem (MacDougal 1925, Arcikhovskiy 1931, Dobbs and Scott 1971, Molz and Klepper 1973, Molz et al. 1973, Lassoie 1973, 1979, Hellkvist et al. 1974, Braekke and Kozlowski 1975, Hinckley and Bruckerhoff 1975, Vogel 1994). These changes can be either positive (increases due to growth or rehydration) or negative (decreases due to dehydration). Irvine and Grace (1997) demonstrated that dimensional changes are not restricted to tissues external to the sapwood; however, as pointed out by Zweifel et al. (2000), these sapwood dimensional changes are small when

Table 3. Water turnover rate, i.e., theoretical mean time during which transpiration can be supported by free water storage in different tree parts and tissues of Douglas-fir 1373 (values of total water storage for corresponding tree parts were taken from Table 1).

Tree part	Time interval	Stem (xyl + phl)	Branch (xyl + phl)	Sapwood (stem + bran)	Phloem (stem + bran)	Needles	Tree total
Upper crown	Days	0.228	0.073	0.255	0.055	0.064	0.374
	Hours	5.5	1.8	6.1	1.3	1.5	9.0
Entire tree	Days	6.57	0.36	6.12	0.81	0.236	7.17
	Hours	158	9	147	19	6	172

compared with those of tissues external to the sapwood. Changes in stem dimensions are useful for modeling and recording stem water potentials, particularly if lags are incorporated (e.g., Zaerr 1971, Molz and Klepper 1973, So 1979, Herzog et al. 1995, Irvine and Grace 1997, Zweifel et al. 2000. Intrigliolo and Castel 2006).

Changes in response to hydration are attributed to the lateral transfer of water between these tissues and the conducting xylem (Molz and Klepper 1973). Hinckley and Bruckerhoff (1975) in white oak, Lassoie (1979) in Douglas-fir and Antonova et al. (1995) in Scots pine noted three general patterns of dimensional changes in trees during the growing season. First, during periods of high soil water content and low evaporative demand, stem diameter increased from one morning to the next and often during the day there was either no decrease or just a reduction in the rate of increase in diameter. This pattern was largely characterized by growth. Second, during periods of high soil water content and high evaporation demand, there was an increase in stem diameter from one morning to the next, but during the day there could be an appreciable decrease. A mixture of growth and tissue rehydration characterized this pattern. Third, during periods of low soil water content and high evaporation demand, there was a daytime reduction in stem diameter with only partial recovery overnight. Only changes in hydration characterized the last pattern. We observed only Pattern 2 in Psme 1373. Recently, these three elements have been integrated in a model (Steppe and Lemeur 2004).

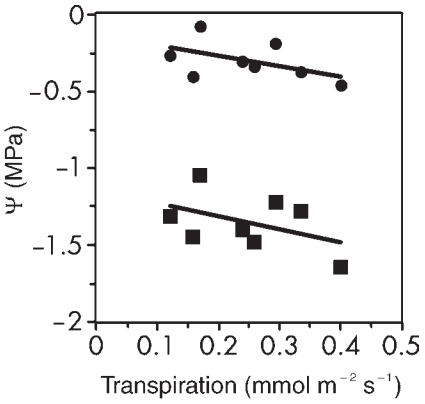

Figure 9. Relationship between transpiration (mmol m^{-2} s^{-1}) and water potential (Ψ, MPa) in the exposed upper crown of old-growth Douglas-fir trees. Each value is the mean of two readings on each of three trees and three measurement days. Short distance hydraulic resistance (●) is the slope of the regression for Ψ of uncovered leaves at solar noon minus Ψ of aluminum-foil-covered leaves Ψ versus the uncovered foliage's transpiration rate. Long distance hydraulic resistance (■) is similarly determined, except the values shown are the Ψ of uncovered leaves at solar noon minus the Ψ of covered leaves at predawn versus the corresponding solar noon values of transpiration in the uncovered foliage (it was assumed that transpiration in the covered foliage was zero).

Seasonal changes in daily water storage and stem volume

A critical assumption in our calculations of the total amount of stored water was that there was no net change from day-to-day (i.e., complete refilling occurred). Three lines of evidence suggested that this assumption was likely justified: first, predawn water potentials were consistently high in Psme 1373 (as well as other Douglas-fir trees measured within the crane circle), second, plotting the radial changes from day-to-day did not demonstrate a progressive decline in radius, and third, on August 8, we added over 800 liters (8.5 mm) of water to the soil surrounding the study tree in an effort to reduce any water deficits. Loustau et al. (1996) made a similar assumption in their calculations for the water relations of *Pinus maritima* Poir. During an extraordinarily dry summer, Hinckley and Bruckerhoff (1975) noted a continuous loss of stem diameter in a white oak tree. They assumed that day-to-day volume changes in extensible tissues reflected a net loss in stem water content—these day-to-day decreases were linearly related to decreases in predawn water potential. Similarly, Waring and Running (1978) observed a progressive decrease in sapwood water content over the growing season in old-growth Douglas-fir trees; maximum water contents of 100% saturation were observed in late February and March and a minimum of 50% was reached in mid-August. Similar conclusions were drawn by Čermák and Nadezhdina (1998) for adult Norway spruce trees, where sapwood was maximally hydrated in early spring and dehydrated substantially, especially in the inner sapwood, during a summer drought. Similar results were found in broadleaf species (Tatarinov and Čermák 1999). These and other studies indicated that our assumption of no net change in tissue water content might have resulted in a slight overestimation of the daily water use from storage: however, predawn water potential did not change appreciably during the summer in our study trees.

Although the total change in water volume (i.e., the amount used) in elastic tissues of the stem was small and mostly constant over the growing season (about 6 dm^3 for the whole trees and 0.3 dm^3 for the treetop; see Figures 6 and 8), daily total

Table 4. Comparison of estimates of water used from storage in various tree species.

Species	Height (m)	Age (year)	Quantity (dm^3 day^{-1}) (%)	Reference
Acer saccharum Marsh.	> 9	30–100	Not given (17%)	Tyree et al. 1991
Anacardium excelsum (Bertero and Balb. ex. Kunth) Skeels.	35	Mature	54 (14%)	Goldstein et al. 1998
Carya illinoensis Wangenh.	4	5	4 (3%)	Steinberg et al. 1990
Cecropia longipes Pittier.	18	Mature	4.0 (9%)	Goldstein et al. 1998
Ficus insipida Willd.	30	Mature	25 (15%)	Goldstein et al. 1998
Larix decidua Mill.	18	70	18 (4%)	Schulze et a l. 1985
Luehea seemannii Triana.	29	Mature	16 (12%)	Goldstein et al. 1998
Malus pumila Mill.	2.5	9	0.7 (20%)[1]	Landsberg et al. 1976
Nothofagus fusca (Hook F.) Oerst.	34	300–400	5–10 (4–8%)	Köstner et al. 1992
Picea abies (L.) Karst.	30	80	9 (14%)	Schulze et al. 1985
Picea abies (L.) Karst.	0.6–1.2	4–6	(2–15%)	Zweifel et al. 2000
Pinus maritima Mill.	24	64	10–13	Loustau et al. 199
Pinus sylvestris L.	15	41	20–30 (30–50%)	Waring et al. 1979
Prunus avium L.	6	15	1 (min 4%)	Čermák et al. 1976
Pseudotsuga m.1373	57	450+	40–70 (20–30%)	This study
Pseudotsuga m. 091	65	450+	22–74 (29–17%)	Phillips et al. 2003
Pseudotsuga menziesii (Mirb.) Franco.	19,15, 6	40	1.8, 1.0, 0.1 (5%)	Lassoie 1979
Quercus robur L.	32	100	10–31 (15–22%)	Čermák et al. 1982
Salix fragilis L.	10	30	3% (1% stem vol)	Čermák et al. 1984
Schefflera morototoni (Aubl.) Maguire, Steyerm. and Frodin.	20	Mature	0.9 (2.5%)	Tyree et al. 1991
Spondias mombin L.	23	Mature	8.7 (11%)	Goldstein et al. 1998
Thuja occidentalis L.	10	Not given	2.5 (22%)	Tyree 1988

[1] Estimated as 2 h of transpiration divided by a nominal 10 h.

water used from storage was much greater and increased as the season proceeded (from about 35 to 55 dm^3). Most of the stored water in the study tree was located in the relatively rigid stem sapwood below 46 m. Water released by cavitation of vascular elements may prevent desiccation of leaves and other living tissues (Dixon et al. 1984, Tyree and Yang 1990) but the loss of hydraulic conductivity due to cavitation may result in further decreases in water potential leading to runaway xylem cavitation (Sperry 1995). However, a balance seems to exist between use of water from cavitated elements and loss of hydraulic conductivity due to cavitation (Sellin 1991*a*, Čermák and Nadezhdina 1998, Sperry et al. 1998, Domec and Gartner 2001).

There is increasing evidence that in large trees sapwood hydraulic capacity maybe vastly more than sufficient to meet transpiration needs under favorable conditions. In *Quercus robur* L. and *Laurus azorica* (Seub.) Franco, it was found that only about 2% of all stem xylem conducting elements were theoretically needed to supply water for rapid transpiration (Krejzar and Kravka 1998, Čermák et al. 2001 and Morales et al. 2001), whereas almost 100% of all conducting xylem elements must function in petioles. Theoretically, the majority of conducting elements in stems could be embolized without significantly affecting stem hydraulic conductivity. For *Laurus azorica*, stem vessels represented the largest store of free water. Because the sapwood does not conduct water uniformly with depth (Swanson 1971, Čermák et al. 1984, 1992, 2004, Phillips et al. 1996, Čermák and Nadezhdina 1998, Jimenez et al. 2000, Nadezhdina et al. 2001), and does not dehydrate uniformly with depth (Čermák and Nadezhdina 1998) it should become a more important source of water as sapwood depth and volume increase. Under such circumstances, the less-conducting part of the sapwood can serve as a source of stored water, while having a minimal impact on hydraulic conductivity. If such stored water is used more than once, cavitated elements must be refilled. Domec and Gartner (2002) suggested that the latewood, because of the smaller diameter of its conductive elements and is greater resistances to flow, may cavitate first and provide water to the transpiration stream. Loss of latewood would not severely impact whole sapwood water conduction.

Waring and Running (1978) hypothesized that refilling of cavitated xylem conduits occurs over winter. However, more recent evidence suggests that refilling of cavitated elements may occur diurnally (Zwieniecki and Holbrook 1998, Holbrook et al. 2002). Irvine and Grace (1997) noted a linear relationship between xylem dimension and xylem water potential, suggesting water loss of individual xylem elements and dimensional changes as a result of the loss. They hypothesized that the conducting xylem could lose volume without cavitating. Second, their study suggests that water can be released in this way within the normal range in plant water potentials. Recently, using snap-freezing of roots and stems and cryo-scanning electromicroscopy, Shane and McCully (1999) and McCully (1998, 1999) observed that as many as 60% of the stem or root conducting vessels may be cavitated. They also observed rapid refilling of cavitated vessels, thereby offering a much more dynamic view of the role and behavior of water in conducting elements. Both the refilling of cavitated elements and the release of water by conducting elements without cavitation needs further study.

In summary, diurnal and seasonal changes in stored water are reflected in decreases in sapwood water content (e.g., Waring and Running 1978, Čermák and Nadezhdina 1998), volumetric changes in elastic tissues (MacDougal 1925, Stewart 1967, Molz and Klepper 1973, Morikawa 1974, Hinckley and Bruckerhoff 1975) and volumetric changes in mature xylem elements (Zimmermann 1983, Irvine and Grace 1997). In general, the water used from storage on any given day is rather small compared with the volume of free water in the tree.

Water turnover rate

On a whole-tree basis, the stem was about 18 times more important in supplying water for transpiration than the branches, but only three times greater if only the upper crown was considered (Table 4). Its sapwood was about 7.5 times more important than phloem, although this difference was reduced to about 4.6 times when only the upper crown was considered. The needle compartment shared a simlar relative importance to that of the branches or phloem. The length of time for which free water can supply transpiration from storage was much longer than that estimated for herbaceous plants (e.g., Rychnovska et al. 1980), but similar to values mentioned for other woody species.

Hydraulic resistance

Our results confirm the need to account for hydraulic architecture, including the distribution of storage elements, in whole-tree process modeling (Tyree 1988). Friction during high rates of transpiration adds a significant constraint that is manifested in the form of greater tensions or more negative water potentials at the tops of tall trees (Bauerle et al. 1999, Koch et al. 2004, Woodruff et al. 2004). The increase in water potential gradients with transpirational water movement, however, followed a constant resistance for both short and long distances (cf. Camacho et al. 1974, Wenkert 1983, Ryan et al. 2000). Although our data followed a simple constant resistance analog (see Figure 9), the combination of long distance sap transport components caused branchlet water potential to fall below –1.5 MPa at the treetops. Recently, Woodruff et al. (2004) concluded that the gravitational component of water potential is a significant contributor to the decline in leaf turgor with increasing height. Although the gravitational component of water potential contributes 0.01 MPa m^{-1} to the xylem tension gradient, our data indicate that the frictional potential added yet another negative constraint that can decrease leaf water potential and affect leaf turgor, further supporting the hydraulic limitation hypothesis of Ryan and Yoder (1996). For Psme 1373, the observed leaf specific conductivity was 1.132 mmol m^{-2} s^{-1} MPa^{-1} and was slightly greater (i.e., less resistance) than the value of ~0.8 mmol m^{-2} s^{-1} MPa^{-1} reported by Irvine et al. (2004) in old-growth ponderosa pine. Irvine et al. (2004) also observed that LSC was six times greater in young, smaller trees than in tall, old trees.

In conclusion, tissues of old-growth Douglas-fir trees contain large amounts of free water. Stem sapwood appears to be the most important, followed by stem phloem, branch sapwood, branch phloem and needles. There are significant time lags (minutes to hours) between sap flows measured at different positions within the transport system (i.e., stem base to shoot tip). These shifts suggest that the transport system is highly elastic. Moreover, on clear days, the daily quantity of water used from storage ranges from 25 to almost 75 liters (i.e., about 20 to 30% of daily sap flow). Our results suggest that the source of this water varies spatially and the greatest amount of water comes from the lower stem; however, more water is transpired from the tree top. In addition to positional lags in stem flow, the withdrawal and refilling of water storage components is reflected in changes in stem volume. There is a strong linear relationship between volume changes and transpiration when time shifts (minutes to hours near the top and the base of the stem, respectively) are considered. The volume changes are small (only about 14%) compared with the amount of stored water used daily, indicating that most of the stored water comes from inelastic tissues (i.e., sapwood), which can supply water for transpiration of the whole tree for about a week, but only for several hours from tissues in the upper crown taken separately. The disproportionate use of stored water from the top of the tree, the drier microclimate of the upper canopy, and the more negative water potentials found in the tops of tall trees appear to cause greater desiccation and resultant top-dieback.

Acknowledgments

The authors thank Dr. David Shaw, Mr. Buz Baker and Mr. Mark Creighton for their assistance at the Wind River Canopy Crane Research site. Ms. Sarah McCarthy provided needle water content data and Drs. Horaki Ishii and Nate McDowell provided leaf area data. This research was supported by the Biological and Environmental Research Program (BER), U.S. Department of Energy, through the Western Regional Center of the National Institute for Global Environmental Change (NIGEC) under Cooperative Agreement No. DE-FC03-90ER61010. The authors also thank the U.S. Forest Service for providing the Rose Canopy Platform.

References

Antonova, G.F., V.P. Cherkashin, V.V. Stasova and T.N. Varaksina. 1995. Daily dynamics in xylem cell radial growth of Scots pine (*Pinus sylvestris* L.). Trees 10:24–30.

Arcikhovskiy, V.M. 1931. Suction of water by woody species under its artificial injection through holes in conducting tissues. Trudy po lesnomu opytnomu delu, CLOS, XI: 69–141. In Russian.

Bauerle, W.L., T.M. Hinckley, J. Čermák, J. Kučera and K. Bible. 1999. The canopy water relations of old-growth Douglas-fir trees. Trees 13:211–217.

Borchert, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75: 1437–1449.

Braekke, F.H. and T.T. Kozlowski. 1975. Shrinkage and swelling of system of *Pinus resinosa* and *Betula papyrifera* in northern Wisconsin. Plant Soil 43:387–410.

Brooks, J.R., P.J. Schulte, B.J. Bond, R. Coulombe, J.C. Domec, T.M. Hinckley, N. McDowell and N. Phillips. 2003. Does foliage on the same branch compete for the same water? Experiments on Douglas-fir trees. Trees 17:101–108.

Camancho-B., S.E., A.E. Hall and M.R. Kaufman. 1974. Efficiency and regulation of water transport in some woody and herbaceous species. Plant Physiol. 54:169–172.

Čermák, J. and J. Kučera. 1981. The compensation of natural temperature gradient in the measuring point during the sap flow rate determination in trees. Biol. Plant. 23:469–471.

Čermák, J. and J. Kučera. 1990. Changes in transpiration of healthy mature trees due to environmental conditions and of those with damaged water conductive system. *In* Proc. IUFRO Internat. Workshop Verification of hypotheses and possibilities of recovery of forest ecosystems. Eds. E. Klimo and J. Materna. Beskydy Mt., Czechoslovakia, Sept. 4–8, 1989. Agr. Univ. Brno, pp. 275–286.

Čermák, J. and N. Nadezhdina. 1998. Sapwood as the scaling parameter—defining according to xylem water content or radial pattern of sap flow? Ann. Sci. For. 55:509–521.

Čermák, J., M. Deml and M. Penka. 1973. A new method of sap flow rate determination in trees. Biol. Plant. (Praha) 15:171–178.

Čermák, J., M. Palát and M. Penka. 1976. Transpiration flow rate in fully-grown tree *Prunus avium* L. by heat balance method estimated, in connection with some meteorological factors. Biol. Plant. (Praha) 18:111–118.

Čermák, J., J. Úlehla, J. Kučera and M. Penka. 1982. Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. Biol. Plant. 24: 446–460.

Čermák, J., J. Jeník, J. Kučera and V. idek. 1984. Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. Oecologia 64:145–151.

Čermák, J., E. Cienciala, J. Kučera, A. Lindroth and J.-E. Hallgren. 1992. Radial velocity profiles of water flow in stems of spruce and oak and response of spruce tree to severing. Tree Physiol. 10: 367–380.

Čermák, J., M.S. Jimenez, A.M. Gonzales-Rodriguez and D. Morales. 2001. Laurel forests in Tenerife, Canary Islands: efficiency of water conducting systems in *Laurus azorica* trees. Trees 16: 538–546.

Čermák, J., J. Kučera and N. Nadì dina. 2004. Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. Trees 18:529–546.

Dixon, M.A., J. Grace and M.T. Tyree. 1984. Concurrent measurements of stem density, leaf and stem water potential, stomatal conductance and cavitation on a sapling of *Thuja occidentalis* L. Plant Cell Environ. 7:615–618.

Dobbs, R.C. and D.R.M. Scott. 1971. Distribution of diurnal fluctuations in stem circumference of Douglas-fir. Can. J. For. Res. 1:80–83.

Domec, J.C. and B.L. Gartner. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. Trees 15:204–214.

Domec, J.C. and B.L. Gartner. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? J. Exp. Bot. 53: 2369–2379.

Elfving, D.C., M.R. Kaufmann and A.E. Hall. 1972. Interpreting leaf water potential measurements with a model of the soil-plant-atmosphere continuum. Physiol. Plant. 27:161–168.

Franco-Vizcaino, E., G. Goldstein and I.P. Ting. 1990. Comparative gas exchange of leaves and bark in three stem succulents of Baja California. Am. J. Bot. 77:1272–1278.

Gartner, B.L. 1995. Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp 125–149.

Goldstein, G., F. Meinzer and M. Monasterio. 1984. The role of capacitance in the water balance of Andean giant rose species. Plant Cell Environ. 6:649–656.

Goldstein, G., J.L. Andrade, F.C. Meinzer, N.M. Holbrook, J. Cavelier, P. Jackson and A.Celis. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ. 21:397–406.

Hellkvist, J., G.P. Richards and P.G. Jarvis. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. 11:637–668.

Herzog, K.M., R. Häsler and R. Thum. 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, T.M. and D.N. Bruckerhoff. 1975. The effect of drought on water relations and stem shrinkage of *Quercus alba*. Can. J. Bot. 53:62–72.

Hinckley, T.M., J.R. Brooks, J. Čermák, R. Ceulemans, J. Kucera, F.C. Meinzer and D.A. Roberts. 1994. Water flux in a hybrid poplar stand. Tree Physiol. 14:1005–1018.

Holbrook, N.M. 1995. Stem water storage. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp.151–174.

Holbrook, N.M. and T.R. Sinclair. 1992*a*. Water balance in the arborescent palm, *Sabal palmetto*. I. Stem structure, tissue water release properties and leaf epidermis conductance. Plant Cell Environ. 15:393–399.

Holbrook, N.M. and T.R. Sinclair. 1992*b*. Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and stem water storage. Plant Cell Environ. 15:401–409.

Holbrook, N.M., M.A. Zwieniecki and P.J. Melcher. 2002. The dynamics of "dead wood:" Maintenance of water transport through plant stems. Integrative Compar. Biol. 42:492–496.

Intrigliolo, D.S. and J.R. Castel. 2006. Usefulness of diurnal trunk shrinkage as a water stress indicator in plum trees. Tree Physiol. 26: 303–311.

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

Irvine, J., B.E. Law, M.R. Kurpius, P.M. Anthoni, D. Moore and P.A. Schwarz. 2004. Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine. Tree Physiol. 24:753–763.

Ishii, H., J.H. Reynolds, E.D. Ford and D.C. Shaw. 2000. Height growth and vertical development of an old-growth Pseudotsuga-Tsuga forest in southwestern Washington State, U.S.A. Can. J. For. Res. 30:17–24.

Ishii, H., E.D. Ford, M.E. Boscolo, A.C. Manriquez, M.E. Wilson and T.M. Hinckley. 2002. Variation in specific needle area of old-growth Douglas-fir in relation to needle age, within-crown position and epicormic shoot production. Tree Physiol. 22:31–40.

Jimenez, M.S., N. Nadezhdina, J. Čermák and D. Morales. 2000. Radial variation of sap flow in five laurel forest tree species in Tenerife, Canary Islands. Tree Physiol. 20:1149–1156.

Klepper, B., D. Browning and H.M. Taylor. 1971. Stem diameter in relation to plant water status. Plant Physiol. 48:683–685.

Koch, G.W., S.C. Sillett, G. Jennings and S.B. Davis. 2004. The limits to tree height. Nature 428:851–854.

Korf, V., K. Hubac, S. Smelko and J. Wolf. 1972. Dendrometry. In Czech. State Agricultural Press (SZN), Prague, 378 p.

Köstner, B.M.M., E.-D. Schulze, F.M. Kelliher, D.Y. Hollinger, J.N. Byers, J.E. Hunt, T.M. McSeveny, R. Meserth and P.L. Weir. 1992. Transpiration and canopy conductance in a Pristine broad-leaved forest of Nothofagus—an analysis of xylem sap flow and eddy correlation measurements. Oecologia 91:350–359.

Kučera, J., J. Čermák and M. Penka. 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. Biol. Plant. 19:413–420.

Kravka, M. and J. Čermák. 1995. Water storage in stem wood of large pine and spruce trees in central Sweden natural forests. European Geophysical Society, Proc. XX General Assembly, Annales Geophysicae. Part II. Oceans, Atmosphere, Hydrology & Nonlinear Geophysics, Suppl. II to Vol. 13, p. C-504, Hamburg, Germany.

Kravka, M., T. Krejzar and J. Čermák. 1999. Water content in stem wood of large pine and spruce trees in natural forests in central Sweden. Agric. For. Meteorol. 98–99:555–562.

Krejzar., T. and M. Kravka. 1998. Sap flow and vessel distribution in annual rings and petiols of large oaks. Lesnictvi-Forestry 44:193–201.

Ladefoged, L. 1963. Transpiration of forest trees in closed stands. Physiol Plant. 16:378–414.

Landsberg, J.J., T.W. Blanchard and B. Warrit. 1976. Studies on movement of water through apple trees. J. Exp. Bot. 27:579–596.

Lassoie, J.P. 1973. Diurnal dimensional fluctuations in a Douglas-fir stem in response to tree water status. For. Sci. 19:251–255.

Lassoie, J.P. 1979. Stem dimensional fluctuations in Douglas-fir stem in response to tree water status. For. Sci. 25:132–144.

Lindroth, A., J. Čermák, J. Kučera, E. Cienciala and H. Eckersten. 1995. Sap flow by heat balance method applied to small size salix-trees in a short-rotation forest. Biomass Bioenergy 8:7–15.

Long, J.N., F.W. Smith and D.R.M. Scott. 1981. The role of Douglas-fir stem sapwood and heartwood in the mechanical and physiological support of crowns and development of stem form. Can. J. For. Res. 11:459–464.

Loustau, D., P. Berbegier, R. Roumangnac, C. Arruda-Pecheco, J.S. David, M.I. Ferreira, J.S. Perreira and R. Tavares. 1996. Transpiration of a 64-year-old Maritime pine stand in Portugal. 1. Seasonal course of water flux through Maritime pine. Oecologia 107:33–42.

MacDougal, D.T. 1925. Reversible variations in volume, pressure and movements of sap in trees. Carnegie Inst. Washington, Publ. No. 365, 90 p.

Martin, T.A., K. Brown, J. Čermák, R. Ceulemans, J. Kučera, R. Meinzer, J. Rombolt, D. Sprugel and T.M. Hinckley. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. Can. J. For. Res. 27:797–808.

Martin, T.A., K.J. Brown, T.M. Hinckley, J. Kučera, F.C. Meinzer and D.G. Sprugel. 2001. Control of transpiration in a 220-year-old *Abies amabilis* forest. For. Ecol. Manage. 152:211–224.

McCully, M.E. 1998. Daily embolism and refilling of xylem vessels in the roots of field-grown maize. New Phytol. 138:327–342.

McCully, M.E. 1999. Root xylem embolism and refilling. Relation to water potentials of soil, roots and leaves and osmotic potentials of root xylem sap. Plant Physiol. 119:1001–1008.

McDowell, N.G., H. Barnard, B.J. Bond et al. 2002. The relationship between tree height and leaf area: sapwood area ratio. Oecologia 132:12–20.

Meinzer, F.C., J.R. Brooks, J.C. Domec, B.L. Gartner, J.M. Warren, D.R. Woodruff, K. Bible and D.C. Shaw. 2006. Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. Plant Cell Environ. 29:105–114.

Milne, . 1989. Diurnal water storage in the stems of *Picea sitchensis* (Bong.) Carr. Plant Cell Environ. 12:63–72.

Molz, F.J., B. Klepper and C.M. Peterson. 1973. Rehydration versus growth-induced water uptake in plant tissues. Plant Physiol. 51: 859–862.

Molz, F.J. and B. Klepper. 1973. On the mechanism of water-stress-induced stem deformation. Agron. J. 65:304–306.

Morales, D., M.S. Jimenez, A. Gonzalez-Rodriguez and J. Čermák. 2001. Forests in Tenerife, Canary Islands: vessel distribution in stems and in petioles of *Laurus azorica* trees. Trees 16:529–537.

Morikawa, Y. 1974. Sap flow in *Chamaecyparis obtusa* in relation to water economy of woody plants. Tokyo Univ. For. Bull. 66: 251–297.

Nadezhdina, N., J. Čermák, D. Morales, M.S. Jimenez, A. Raschi, I. Ferreira. and J. Michaelsen. 2001. Estimation of xylem sap flow conducting patterns in stems of ten tree species growing in three Mediterraen countries as a pre-condition for upscaling data from trees to forest stands. *In* Proc. Int. Conf. For. Res.: A Challenge For an Integrated European Approach. Vol. II. Ed. K. Radoglou. Thesalonniki, Greece, pp 507–512.

Parker, G.G. 1997. Canopy structure and light environment of an old-growth Douglas-fir/western hemlock forest. Northwest Sci. 71:261–270.

Parker, G.G., M.M. Davis and S.M. Chapotin. 2002. Canopy light transmittance in Douglas-fir-western hemlock stands. Tree Physiol. 22:147–157.

Perämäki, M., E. Nikinmaa, S. Sevanto, H. Ilvesniemi, E. Siivola, P. Hari and T. Vesala. 2001. Tree stem diameter variations and transpiration in Scots pine: an analysis using dynamic sap flow model. Tree Physiol. 21:889–897.

Philip, M.S. 1994. Measuring trees and forests. CAB International, Wallingford, University Press, Cambridge, U.K., 310 p.

Phillips, N., R. Oren and R. Zimmermann. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. Plant Cell Environ. 19:983–990.

Phillips, N.G., M.G. Ryan, B.J. Bond, N.G. McDowell, T.M. Hinckley and J. Čermák. 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest Tree Physiol. 23:237–245.

Roberts, J. 1976. An examination of the quantity of water stored in mature *Pinus sylvestris* L. trees. J. Exp. Bot. 27:473–479.

Ryan, M.G. and B.J. Yoder. 1996. Hydraulic limits to tree height and tree growth. Bioscience 47:235–242.

Ryan, M.G., B.J. Bond, R.M. Hubbard, E. Cienciala, J. Kučera, D. Woodruff, B.E. Law and R. Lewis. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. Oecologia 124:553–560.

Rychnovská, M., J. Čermák and P. Šmíd. 1980. Water output in a stand of *Phragmites communis* Trin. A comparison of three methods. Acta Sci. Nat. 14:1–27.

Schulte, P.J. 1993. Tissue hydraulic properties and the water relations of desert shrubs. *In* Water Deficits: Plant Responses from Cell to Community. Eds. J.A.C. Smith and H. Griffiths. BIOS Scientific Publishers, pp 171–191.

Schulze, E.-D., J. Čermák, R. Matyssek, M. Penka, R. Zimmermann, F. Vasicek, W. Gries and J. Kučera. 1985. Canopy transpiration and flow rate fluxes in the xylem of the trunk of *Larix* and *Picea* trees—a comparison of xylem flow, porometer and cuvette measurements. Oecologia 66:475–483.

Sellin, A. 1991*a*. Variation in sapwood thickness of *Picea abies* in Estonia dependinRg on tree age. Scand. J. For. Res. 6:463–469.

Sellin, A. 1991*b*. Hydraulic conductivity of xylem depending on water saturation level in Norway spruce (*Picea abies* (L.) Karst.). J. Plant Physiol. 138:466–469.

Sevanto, S., T. Vesala, M. Perämäki and E. Nikinmaa. 2002. Time lags for xylem and stem diameter variations in a Scots pine tree. Plant Cell Environ. 25:1071–1077.

Shane, M.W. and M.E. McCully. 1999. Root xylem embolisms: implications for water flow to the shoot in single-rooted maize plants. Aust. J. Plant Physiol. 26:107–114.

Shaw, D.C., J.F. Franklin, K. Bible, J. Klopatek, E. Freeman, S. Greene and G.G. Parker. 2004. Ecological setting of the Wind River old-growth forest. Ecosystems 7:427–439.

So, H.B. 1979. An analysis of the relationship between stem diameter and leaf water potential. Agron. J. 71:675–679.

Sperry, J.S. 1995. Limitations on stem water transport and their consequences. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp 105–124.

Sperry, J.S., F.R. Adler, G.S. Campbell and J.P. Comstock. 1998. Limitation of plant water use by rhizosphere and conductance: results from a model. Plant Cell Environ. 21:347–359.

Steinberg, S.L., M.J. McFarland and J.W. Worthington. 1990. Comparison of trunk and branch sap flow with canopy transpiration in Pecan. J. Exp. Bot. 41: 653–659.

Steppe, K. and R. Lemeur. 2004. An experimental system for analysis of the dynamic sap-flow characteristics in young trees: results of a beech tree. Funct. Plant Biol. 31, 83–92.

Stewart, C.M. 1967. Moisture content of living trees. Nature 214: 138–140.

Swanson, R.H. 1971. Velocity distribution patterns in ascending xylem sap during transpiration. *In* Symposium on Flow—Its Measurement and Control in Science and Industry. Canadian Forestry Service Paper No. 4/2/171, 11 p.

Tatarinov, F. and J. Čermák. 1999. Daily and seasonal variation of stem radius in oak. Ann. Sci. For. 56:579–590.

Tatarinov, F., J. Čermák, J. Kučera and A. Prax. 2000. Transpiration of spruce in a mature plantation in Drahanska Vrchovina uplands, Moravia. I. Variation between individual trees. Ekologia (Bratislava) 19:48–62.

Tatarinov, F., J. Kučera and E. Cienciala. 2005. The analysis of physical background of tree sap flow measurements based on thermal methods. Meas. Sci. Technol. 16:1157–1169.

Tyree, M.T. 1988. Dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. Tree Physiol. 4:195–217.

Tyree, M.T. and S. Yang. 1990. Water-storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms. Planta 182: 420–426.

Tyree, M.T., D.A. Snyderman, T.R. Wilmot and J.-L. Machado. 1991. Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*). Plant Physiol. 96:1105–1113.

Vogel, M. 1994. Automatic precision measurement of radial increment in a mature spruce stand and interpretation variants of short-term changes in increment values. In German. Allg. Forst-u. J. Ztg., 1965:34–40.

Waring, R.H. and S.W. Running. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Eviron. 1:131–140.

Waring, R.H., D. Whitehead and P.G. Jarvis. 1979. The contribution of stored water to transpiration in Scots pine. Plant Cell Environ. 2: 309–317.

Wenkert, W. 1983. Water transport and balance within plant: an overview. *In* Limitations to Efficient Water Use in Crop Production. Eds. H.M. Taylor, W.R. Jordon and T.R. Sinclair. American Society of Agronomy, Madison, Wisconsin, pp 137–172.

Woodruff, D.R., B.J. Bond and F.C. Meinzer. 2004. Does turgor limit growth in tall trees? Plant Cell Environ. 27:229–236.

Zaerr, J.B. 1971. Moisture stress and stem diameter in young Douglas-fir. For. Sci. 17:460–469.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, 143 p.

Zimmermann, M.H. and C.L. Brown. 1971. Trees, structure and function. Springer-Verlag, Berlin, 336 p.

Zweifel, R. and R. Häsler. 2001. Dynamics of water storage in mature subalpine *Picea abies*: temporal and spatial patterns of change in stem radius. Tree Physiol. 21:561–569.

Zweifel, R., H. Item and R. Häsler. 2000. Stem radius changes and their relation to stored water in stems of young Norway spruce trees. Trees 15:50–57.

Zweifel, R., H. Item and R. Häsler. 2001. Link between diurnal stem radius changes and tree water relations. Tree Physiol. 21:869–877.

Zwieniecki, M.A. and N.M. Holbrook. 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). Plant Cell Environ. 21:1173–1180.