

Reliance on stored water increases with tree size in three species in the Pacific Northwest

N. G. PHILLIPS,^{1,2} M. G. RYAN,^{3,4} B. J. BOND,⁵ N. G. MCDOWELL,⁵ T. M. HINCKLEY⁶ and J. ČERMÁK⁷

¹ Geography Department, Boston University, Boston, MA 02215, USA

² Author to whom correspondence should be addressed (Nathan@bu.edu)

³ USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80526, USA

⁴ Department of Forest Sciences and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523, USA

⁵ Forest Science Department, Oregon State University, Corvallis, OR 97331, USA

⁶ College of Forest Resources, University of Washington, Seattle, WA 98195, USA

⁷ Institute of Forest Ecology, Mendel University of Agriculture and Forestry, 62 100 Brno, Czech Republic

Received May 16, 2002; accepted August 30, 2002; published online February 3, 2003

Summary In tall old forests, limitations to water transport may limit maximum tree height and reduce photosynthesis and carbon sequestration. We evaluated the degree to which tall trees could potentially compensate for hydraulic limitations to water transport by increased use of water stored in xylem. Using sap flux measurements in three tree species of the Pacific Northwest, we showed that reliance on stored water increases with tree size and estimated that use of stored water increases photosynthesis. For Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), water stored in xylem accounted for 20 to 25% of total daily water use in 60-m trees, whereas stored water comprised 7% of daily water use in 15-m trees. For Oregon white oak (*Quercus garryana* Dougl. ex Hook.), water stored in xylem accounted for 10 to 23% of total daily water use in 25-m trees, whereas stored water comprised 9 to 13% of daily water use in 10-m trees. For ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), water stored in xylem accounted for 4 to 20% of total daily water use in 36-m trees, whereas stored water comprised 2 to 4% of daily water use in 12-m trees. In 60-m Douglas-fir trees, we estimated that use of stored water supported 18% more photosynthesis on a daily basis than would occur if no stored water were used, whereas 15-m Douglas-fir trees gained 10% greater daily photosynthesis from use of stored water. We conclude that water storage plays a significant role in the water and carbon economy of tall trees and old forests.

Keywords: hydraulic capacitance, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Quercus garryana*, sapwood, water storage, xylem.

Introduction

Water flow in trees is subject to frictional resistance that increases with path length (tree height and branch length) and

gravity. As trees grow taller, increasing frictional resistance and gravitational potential may reduce leaf and whole-tree photosynthesis by forcing closure of leaf stomata (Friend 1993, Yoder et al. 1994, Ryan and Yoder 1997), limiting CO₂ supply to sites of photosynthetic fixation, and decreasing photosynthetic carbon reduction (Tezara et al. 1999). Hydraulic, genetic, respiratory and nutritional factors may limit photosynthesis and tree height growth in tall trees (Ryan and Yoder 1997, Becker et al. 2000). All such limitations to photosynthesis in tall trees, and any mechanisms that tend to maintain photosynthesis in tall trees, are crucial to understanding the carbon assimilation potential of forests with tall trees (Suchanek et al. 2002).

Water storage in plants is an adaptation that helps plants overcome drought (Holbrook 1995). Water storage capacity varies considerably among plant species and growth form (Waring and Running 1978, Hunt et al. 1991, Goldstein et al. 1998). Within species, it is not known if use of stored water on a daily basis changes with tree size, if stored water offsets limitations to water transport in tall trees, or if changes in use of stored water with tree size represent an adaptation to hydraulic constraints of tree size or are simply a consequence of tree size. Use of water stored in trunks and branches may allow leaves to operate at water potentials favorable for photosynthesis during peak daylight hours (Goldstein et al. 1998, Stratton et al. 2000, Maherali and DeLucia 2001). Within branches or boles, stored water is derived from the elastic shrinkage of vascular tissues, capillary storage from air–water interfaces within xylem, and from cavitation of water-filled conducting cells (Tyree and Yang 1990). Water storage and hydraulic capacitance are related: hydraulic capacitance is defined as water storage divided by the water potential difference that extracts that stored water. The specific subject of our study was water storage. Variation in water content of wood is largely confined

to the conducting sapwood of trees rather than the nonconducting, inner heartwood (Stewart 1967, Hinckley et al. 1978, Holbrook 1995).

The study objectives were to: (1) quantify the use of stored water in trees; (2) assess whether the use of stored water increases with tree size; and (3) estimate the effect of stored water use on the carbon economy of trees. The study was conducted during the growing season on three species in ecosystems that differ substantially in annual precipitation (Table 1). We measured water flux in boles and crowns of trees of different sizes, where all trees had the same exposure to light. We did not consider water stored in bark, phloem, roots and foliage of trees. Instantaneous differences in water flux between tree crowns and boles over 24-h periods indicated times when water was discharged from, or recharged into, boles of trees.

Materials and methods

Species and sites

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees were located in and near the Wind River Canopy Crane Research Facility in southern Washington State (45°49' 13" N, 121°57' 06" W). The facility is at an elevation of 368 m. Mean annual temperature is 8.7 °C and mean precipitation is 2400 mm. Further site details are provided by Shaw et al. (2002). Three dominant 15-m-tall trees and one dominant 60-m-tall Douglas-fir tree were selected for sap flow measurements during the 1998 and 1999 growing seasons. The 15-m trees were in an even-aged stand about 5 km from the crane

site, at an elevation of 558 m. Additionally, sap flow data from the 1996 summer were available for a 57-m-tall Douglas-fir at the crane site (Čermák et al. 2002).

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) trees were located near Black Butte, Oregon, on the east slope of the Cascade range (44°25' N, 121°40' W), at an elevation of 1030 m. Mean annual temperature is 7.7 °C and mean annual precipitation is 360 mm. Further site details are provided by Ryan et al. (2000). Five open-grown 36-m-tall trees and five open-grown 12-m-tall trees were selected for sap flow measurements during the 1996 growing season.

Oregon white oak (*Quercus garryana* Dougl. ex Hook.) trees were located in the Willamette Valley, Corvallis, Oregon (44°34' N, 123°15' W), at an elevation of 90 m. Mean annual temperature is 11.1 °C and mean annual precipitation is 1085 mm. Three 25-m trees and three 10-m trees, each from even-aged groves located about 100 m apart, were selected for sap flow measurements during the 1999 growing season. Further information about sites, trees, and sap flux measurements is provided in Table 1.

Sap flux measurements

Sap flux sensors were installed in boles and upper branches of trees. Exposed upper branches were chosen to be representative of upper-crown flux. In Douglas-fir trees, the heat dissipation sap flux technique (Granier 1985) was used for all trees except for the 57-m tree from 1996, for which the heat balance technique was used (Kučera et al. 1977). In the 57-m Douglas-fir tree, four sap flux sensors were spaced equally around the bole at a height of 4 m, and eight sap flux sensors

Table 1. Site and tree characteristics, and sap flux sampling measurements. Numbers in parentheses are standard errors.

Site	Species	Dates	Tree age (year)	Tree diameter (m)	Tree height (m)	Site leaf area index	Site stem density > 5 cm (no. ha ⁻¹)	Leaf/sapwood area (m ² cm ⁻²)	Number of trees	Sap flux method ¹	Number of sap flux measurements		
											Outer xylem	Inner xylem	Branches and upper stems
Wind River	Douglas-fir	1998–1999	15	0.18 (0.034)	15	11	3057	0.51 (0.051)	3	HD	2	1	2
			450	1.57	60	9	448	0.39 (0.078)	1	HD	3	2	3
			1996	450	1.30	57	9	448	0.39 (0.078)	1	HB	4	0 ²
Corvallis	Oregon white oak	1999	40	0.23 (0.01)	10	3.2	1200	0.23 (0.02)	3	HD	2	2	2
			250	0.55 (0.05)	25	3.3	140	0.37 (0.01)	3	HD	3	2	2
Black Butte	Ponderosa pine	1996	43	0.27 (0.024)	12	< 1	< 100	0.14 (0.0015)	5	HB	1–4	0 ²	0
			257	0.75 (0.046)	36	< 1	< 100	0.09 (0.0034)	5	HB	1–4	0 ²	0

¹ HD = Heat Dissipation Method; HB = Heat Balance Method.

² Heat balance probes extended across all sapwood in Douglas-fir and nearly across all sapwood in ponderosa pine trees.

were distributed from the base of the live crown (46 m) to the treetop branches. In the 60-m Douglas-fir tree, five sap flux sensors were positioned around the bole at a height of 3 m, at two depths in the 4.7-cm deep sapwood to account for radial flux profiles (Phillips et al. 1996), and three upper-canopy branches were equipped with sap flux sensors. Although three upper-canopy branches represent a small portion of the total crown, correlations between 5-min sap fluxes among branches were high (mean $r^2 = 0.94$ at zero lags), indicating a fairly uniform temporal pattern of within-crown flux for comparison with the time series of bole flux. In each of the three shorter Douglas-fir trees, three sensors were located at about 1.5 m above ground, at two depths within the ~4-cm deep sapwood. The trees were fitted with one sap flux probe in a representative upper branch and one probe in the upper main stem at mid-crown. Correlations among the three upper branches of the 15-m Douglas-fir trees were high (mean $r^2 = 0.96$ at zero lags), indicating a uniform temporal pattern of crown flux. In all Douglas-fir trees, sapwood depth was determined visually by inspection of 5-mm diameter increment cores taken in duplicate from near the vertical position of the sap flux sensors. Because we directly estimated sapwood depth, error in sapwood area estimates per tree was considered negligible. Sap flux data collection in Douglas-fir occurred at time intervals ranging from 30 s to 1 min for all trees and sensors, and values were averaged and stored at intervals ranging from 5 min (60-m and 15-m trees) to 15 min (57-m tree).

In ponderosa pine trees, the heat balance sap flow method was used in boles only. One to four sap flux gauges were placed 2–3 m above ground in each ponderosa pine bole, according to the procedure described by Ryan et al. (2000). Sap flux measurements were collected every minute and averaged and stored every 15 min.

In Oregon white oak, the heat dissipation technique was used. On each 25-m white oak, five sensors were installed in boles about 3 m above ground, covering two depths in the sapwood (mean sapwood depth = 4.9 cm). On 10-m oaks, four sensors were installed in each bole about 1 m above ground, covering two depths in the sapwood (mean sapwood depth = 4.3 cm). In each 10-m and 25-m oak tree, the upper main stem and one upper-crown branch were equipped with sap flux sensors. In both 10-m and 25-m oaks, correlations among upper-crown branch sap fluxes were high (mean $r^2 = 0.95$ and 0.92 at zero lags, respectively), indicating a uniform temporal pattern of crown flux. Sapwood depths were determined directly in 10-m and 25-m trees using one to two increment cores each as described for Douglas-fir. Sap flux measurements were made every 10 s and averaged and recorded every 10 min.

All constant heat sap flux sensors were insulated with foam insulation covered by reflective aluminum foil and clear plastic waterproofing material. Heat dissipation sensors were insulated with reflective bubble wrap extending about 50 cm both above and below the vertical position of the sensors. Branch sap flux sensors were similarly insulated, with the addition of an underlying layer of plumbing pipe insulation.

Temperature differences between heated and reference probes of the heat dissipation sensors were converted to sap flux density (J_s ; $\text{g m}^{-2} \text{ sapwood s}^{-1}$) based on an empirical calibration equation (Granier 1985). Total tree water flux in boles (J ; g s^{-1}) was computed by multiplying flux density by sapwood area. For the heat balance sensors, flux was computed from the stem energy balance equation (Kučera et al. 1977). The 24-h sums of mean branch and upper stem flux in Douglas-fir and Oregon white oak were averaged and set equal to the 24-h sum of bole flux to represent total crown water flux, similar to the approach described by Loustau et al. (1996). Crown flux that exceeded bole flux represented water storage withdrawal, whereas bole flux that exceeded crown flux represented recharge. In ponderosa pine trees, because of a lack of branch-level sap flux sensors, daily stored water use was estimated as the proportion of water taken up by trees after photosynthetically active radiation reached zero in the evening (Morikawa 1974).

To assess the influence of naturally occurring temperature gradients on the function of the heat dissipation sap flux sensors, bole and branch sensors in Douglas-fir were operated without heat on a clear day with high temperature variation. The natural diurnal temperature signals obtained were subtracted from the diurnal temperature signals from a day of nearly identical ambient temperature variation when heat was supplied to the probes. The mean maximum natural temperature gradient observed in a 24-h period in 60-m tree boles was 0.18 ± 0.12 (SD) $^{\circ}\text{C}$ and in 60-m tree branches it was 1.0 ± 0.38 $^{\circ}\text{C}$. The corresponding values for 15-m trees were 0.50 ± 0.17 and 1.2 ± 0.55 $^{\circ}\text{C}$. Sap flux estimates derived from raw temperature diurnal courses and those with temperature diurnals subtracted were highly linearly correlated at zero lag (mean $r^2 = 0.99$ for two boles, $r^2 = 0.96$ for three branches in 60-m trees; mean $r^2 = 0.99$ for three boles; $r^2 = 0.96$ for three branches in 15-m trees), indicating that the temporal pattern of estimated sap flux in Douglas-fir boles and branches was not significantly influenced by naturally occurring temperature gradients. In terms of total daily magnitudes of flux, the impact of natural temperature gradients was to reduce estimates of daily flux by 6% in the 60-m tree and 11% in 15-m trees. We could not apply this correction to the entire time series of daily flux because of the varying pattern of diurnal ambient temperature variation. However, the main purpose of this study was to assess the proportion of daily flux contributed by internal water storage. Because temperature gradients did not affect the temporal pattern of sap flux estimates, estimates of relative differences in branch and bole sap fluxes were robust against the presence of natural temperature gradients. We did not perform a similar analysis on white oak, but because of similar site environmental conditions and insulation methods for sap flux, similar impacts of natural temperature gradients were expected.

Three further methodological issues are important to note. First, it is possible that the use of two types of sap flux sensors (constant heat, heat balance) could lead to different estimated courses of diurnal sap flux (Köstner et al. 1996). Although a

comparison between the two sap flow methods has shown general agreement in the magnitudes and shapes of diurnal time courses of sap flux, the heat balance system showed greater sensitivity to atmospheric vapor pressure deficit than the constant heat sensors (Köstner et al. 1996). We were unable to correct for such an effect in this work, but we note that, for each tree studied, a single type of sap flow system was used, to maintain consistency with respect to measurement technique at the whole-tree scale.

Second, to assess possible differences in the computational procedures for estimating stored water use in ponderosa pine versus Douglas-fir and white oak, additional estimates of stored water use in Douglas-fir and white oak were made based on the same analytical procedure used for ponderosa pine (i.e., analysis of nighttime fluxes as proportions of total daily water use). These additional analyses for Douglas-fir and white oak covered the same time periods during which analyses with bole and branch sensors were performed.

Third, we assumed that 24-h sums of crown water flux equal bole water flux (Schulze et al. 1985, Pallardy et al. 1995, Loustau et al. 1996, Martin et al. 1997, Phillips et al. 1997, Goldstein et al. 1998, Maherali and DeLucia 2001). However, water content in trees often changes on daily and seasonal time scales (e.g., Hinckley and Bruckerhoff 1975, Waring and Running 1978, Waring et al. 1979, Čermák and Nadezhdina 1998). Estimates of daily use of stored water in this study do not reflect possible net daily changes in water content of trees. Implications of this assumption are discussed later.

Stomatal conductance and photosynthesis

To assess the impact of stored water on crown photosynthesis, we estimated daily photosynthesis in Douglas-fir by combining field measurements of crown-level stomatal conductance (G_s , estimated by Phillips et al. 2002) with relationships between leaf-scale stomatal conductance (g_s ; $\text{mol m}^{-2} \text{s}^{-1}$) and photosynthesis (A ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) obtained from another study performed at the same sites as our study (McDowell et al. 2002a). These estimates were made in both saturating and non-saturating light during the growing season when above canopy photosynthetic radiation exceeded $400 \mu\text{mol m}^{-2} \text{s}^{-1}$. Totals of 352 and 199 independent measurements of g_s and A were made on foliage of at least three 60-m and three 15-m trees, respectively. Each measurement comprised the mean of three subsamples. Thus, although this approach employs leaf-scale measurements to estimate crown-level photosynthesis, the number of leaf-scale measurements was high and covered a large range of environmental variation. The resulting equations were:

$$A = 13.39(1 - e^{-7.63g_s}) \quad (1)$$

$$(r^2 = 0.62, P < 0.0001, 60\text{-m trees}),$$

$$A = 14.36(1 - e^{-7.34g_s}) \quad (2)$$

$$(r^2 = 0.63, P < 0.0001, 15\text{-m trees}).$$

Sapwood and leaf area estimates

The physical volume of sapwood that could function as a water storage reservoir was estimated for each study tree. Sapwood volume for stems of Douglas-fir trees was estimated from sapwood depth measurements 1.3 m above ground in combination with published values of sapwood taper for Douglas-fir (Domec and Gartner 2001, Spicer and Gartner 2001). Sapwood volume for stems of ponderosa pine was estimated from sapwood depth measurements at a height of 1.3 m in conjunction with sapwood volume data for ponderosa pine reported by Pruyn et al. (2002). Because of a lack of available sapwood volume data for Oregon white oak, stem sapwood volume for this species was assumed to taper as in Douglas-fir; however, the limitation of this assumption is recognized. To quantify how much leaf area could be supported by water storage, leaf area estimates were made for each study tree. For Douglas-fir and ponderosa pine trees, leaf area was obtained from the allometric relationships between sapwood area and leaf area described by McDowell et al. (2002b) and Ryan et al. (2000), respectively. Leaf area estimates for Oregon white oak trees were obtained by multiplying sapwood areas of each tree by leaf area/sapwood area ratios determined in each of the two groves (0.37 , $\text{SE} = 0.01 \text{ m}^2 \text{ cm}^{-2}$ and 0.23 , $\text{SE} = 0.02 \text{ m}^2 \text{ cm}^{-2}$, for the 25-m and 10-m groves, respectively).

Data analysis

For all species and for each day with data for large and small trees of each species, differences in ratios of storage flux to transpiration were evaluated by the Student's t -test, with trees as replicates. Variance in tree-level water flux was considered to result primarily from the variance in sap flux density, J_s , and not variance in sapwood area, because sapwood area was determined directly for each study tree. Because of low replication in the 60-m Douglas-fir trees ($n = 2$, and for only a subset of the record), the standard deviation of the storage flux to transpiration ratio was assumed to equal the difference between the ratios of the two trees during days when data were available for both trees.

Results

The time series of water fluxes in crowns and boles showed that larger trees used a greater proportion of internal water storage in total daily water use than smaller trees (Figures 1 and 2). This difference was observed in both the early and late growing season (Figures 1 and 2). Late-season drought increased the dependency of both smaller trees (except for Douglas-fir) and larger trees on internal water stores (Figure 3), but more so in larger trees (Figure 3). In tall Douglas-fir trees, the proportion of daily water use obtained from storage increased from 20% in the early season to 25% in the late season, whereas small trees maintained a uniform average of 7.2%. Differences in stored water use between 15-m and 60-m Douglas-fir trees were highly significant (Figure 3A, lower panel). In tall Oregon white oak, the proportion of daily water use obtained from storage increased from 10% in the early sea-

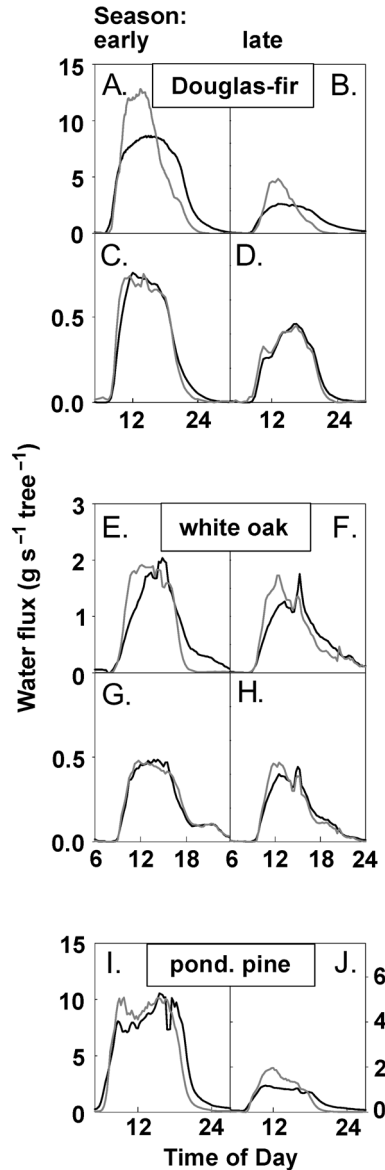


Figure 1. Time courses of sap flow in large (A, B) and small (C, D) Douglas-fir, large (E, F) and small (G, H) Oregon white oak and large and small ponderosa pine (I, J) trees, comparing early season conditions (left-hand panels) with late season conditions (right-hand panels). Data are from representative trees from each species and size class. Gray lines (A–H) represent crown sap flux, and solid lines (A–H) represent bole sap fluxes. Bole fluxes in both size classes of ponderosa pine are shown (I, J), with 12-m trees represented by gray lines and 34-m trees by solid lines.

son to 23% in the late season, whereas small oak trees showed an increase from 9% in the early season to 13% in the late season. Differences in stored water use by 10-m and 25-m white oak were significant during the late season (with the exception of the last few measurement days when total daily fluxes were low), but not early in the season (Figure 3B, lower panel). In tall ponderosa pine trees, the proportion of daily water use obtained from storage increased curvilinearly from 4.0% in the

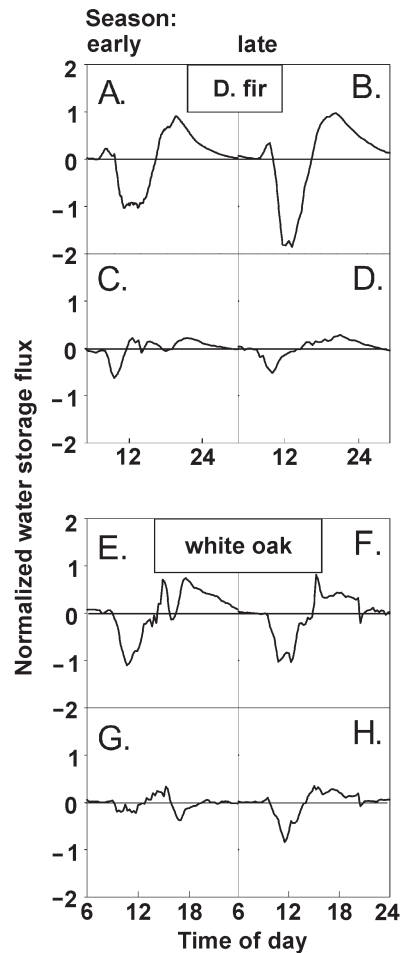


Figure 2. Depletion and recharge of tree water computed from data in Figure 1. Values less than zero indicate periods in which water is withdrawn from trees; values greater than zero indicate periods of tree water recharge. To indicate the relative magnitudes of discharge and recharge, all flux values are normalized by the mean flux rate of the 24-h periods shown. Panels A–H correspond to the similarly labeled panels in Figure 1. Fluxes are not shown for ponderosa pine because these trees lacked upper-crown sap flux sensors.

early season to 20% in the late season, whereas short trees showed an increase from 1.5% in the early season to 4.4% in the late season. Differences in stored water use by 12-m and 36-m ponderosa pine were generally significant throughout the season (Figure 3C, lower panel). Nonsignificant differences were usually associated with cloudy days when total daily water flux was relatively small. Table 2 summarizes the seasonal means of these quantities of stored water.

Estimates of water storage for the study species could depend on whether analyses used nighttime water flux divided by total 24-h flux (ponderosa pine), or sums of instantaneous differences between branch and bole sap flux sensors (Douglas-fir and Oregon white oak). When the method for computing use of stored water in ponderosa pine was applied to Douglas-fir and Oregon white oak, results were in general agreement with the analyses for Douglas-fir and white oak

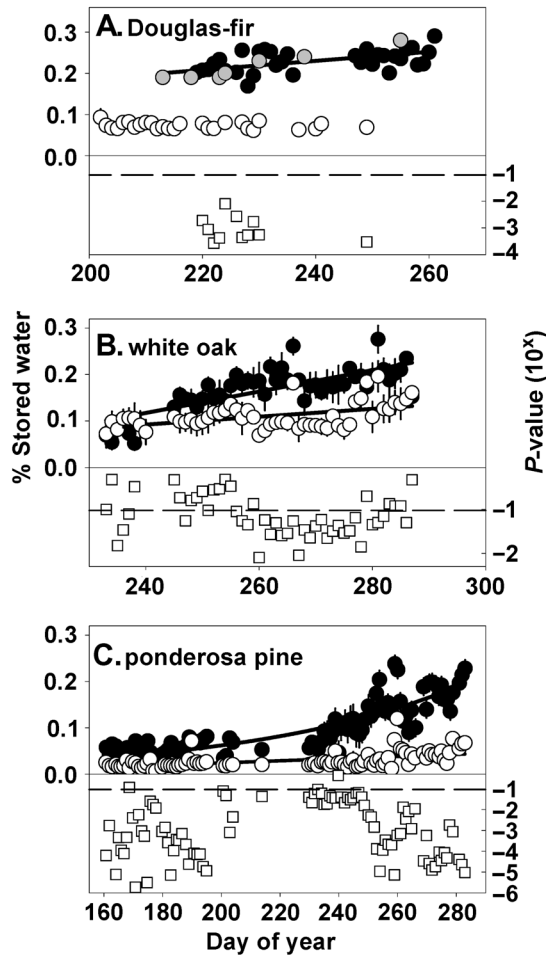


Figure 3. Ratios of daily bole storage flux to daily transpiration flux, in (A) Douglas-fir, (B) Oregon white oak and (C) ponderosa pine trees. Values represent means of tree-level data. In all panels, black or gray symbols represent large trees and open symbols represent small trees. Gray symbols in (A) are derived from data on a 57-m tree in 1996; black symbols in (A) are derived from a 60-m tree in 1998. Standard error bars smaller than graph symbols are not shown. Standard errors of the means for the two large trees in A were not calculated. Adjoined lower panels in (A), (B) and (C) show P -values indicating significant differences between values above.

based on bole and branch sap flux data. In large Douglas-fir, use of the nighttime water flux divided by total 24-h flux method yielded estimates of percent stored water use from

19% in the early season to 22% in the late season (compared with 20 to 25% estimated by the branch-bole method, cited above). Small Douglas-fir trees showed a mean stored water use of 10% (compared with 7% cited above) and, consistent with the prior results, the percentage did not increase over the growing season ($P = 0.66$). Percent water storage in large white oak estimated by the nighttime water flux divided by total 24-h flux method ranged from 7 to 22% from early to late season (compared with 10 to 23% cited above); and small white oak trees used 7 to 15% stored water from early to late season (compared with 9 to 13% cited above).

Discussion

We found that the discharge and recharge of stored water on a diel time scale constitutes a significant portion of the total daily tree water uptake, and that dependency of trees on stored water on diel time scales increases with both tree size and drought. Longer term (days to weeks) changes in the water content of trees, which could contribute substantially to the total water storage capacity, were not considered in this study. It is difficult to assess what proportion of diurnal water use can be attributed to long-term depletion of tree water content. For example, Schulze et al. (1985) found no differences in total daily water flux at the base of the live crown of a 20-m-tall *Larix leptolepis* × *decidua* tree, indicating complete recharge over a 24-h period. In contrast, Constantz and Murphy (1990) found large daily changes in wood water content in a *Juglans regia* L. tree after an irrigation event. Similarly, Waring and Running (1978) show that sapwood relative water content (volume of water divided by volume of air spaces in sapwood) in large Douglas-fir trees can decrease by as much as 5% per day on clear days of high evaporative demand immediately after substantial rain events. For our large Douglas-fir trees, we calculated that such a change represents a net daily water loss of about 28 kg, compared with a maximum daily water use of 395 kg, or 7% of total daily water use. However, this value likely represents an upper limit to the contribution of long-term water storage to daily transpiration, because our study concentrated on relatively late-season conditions when there was little rainfall at any of the study sites (for oak, 19 mm fell in 51 days; for pine, 28 mm fell in 90 days; for Douglas-fir, 69 mm fell in 42 days in the case of 60-m trees, and 12 mm fell in 49 days in the case of 15-m trees). Data from Waring and Running (1978) show little change in relative water content of

Table 2. Summary of sap flux results. Numbers in parentheses are standard errors.

Site	Species	Size class (m)	Mean water use (kg day^{-1})	Maximum water use (kg day^{-1})	Mean water use from storage (% of daily)	Range of water use from storage (% of daily)
Wind River	Douglas-fir	15	14.3 (2.4)	22.0 (3.6)	7.2	7.2–7.2
		60	205 (41)	333 (35)	23	20–25
Corvallis	Oregon white oak	10	14.2 (4.3)	20.0 (5.9)	11	9–13
		25	38.0 (11)	50.3 (20)	17	10–23
Black Butte	Ponderosa pine	12	84 (11)	97 (11)	3	1.5–4.4
		36	167 (16)	183 (16)	10	4.0–20

large Douglas-fir trees after the large short-term responses to rain events. Nevertheless, the water storage data from this study should be considered conservative in that they exclude contributions of net daily water content changes, as well as contributions from bark, roots, small branches, and foliage. Other studies have found large contributions to total tree capacitance from both foliage (Zweifel et al. 2001) and upper branches (Schulze et al. 1985).

Increased use of stored water in larger trees could be an adaptation to, or simply a consequence of, tree size. As trees grow, the ratio of girth to height generally increases (Niklas 1994), presumably as an adaptation for mechanical stability. A byproduct of this structural change in trees is an increase in the bole volume to height ratio, which may result in an increased water storage capacity. However, our estimates of sapwood volume to total bole volume indicate that smaller trees had larger ratios of sapwood volume to bole volume than larger trees ($P < 0.00001$, Figure 4A). If water storage were simply a byproduct of this structural difference between large and small trees, we would predict less, not more water storage capacity relative to tree size as tree size increases. An indication that water storage is more likely an adaptation to hydraulic constraints of tree size is shown by the ratio of tree sapwood volume to leaf area (Figure 4B). Larger trees had significantly greater ratios of sapwood volume to crown leaf area than smaller trees ($P < 0.00001$). Increases in sapwood volume to leaf area ratio were matched by increases in the mean seasonal ratio of daily storage flux to daily transpiration (Figure 5), although relationships differed among species. Thus, it appears that larger trees have a greater water storage capacity relative to water use than smaller trees. Furthermore, water in sapwood of large trees may have a less negative water potential and hence be more easily released to the transpiration stream than in smaller trees (Domec and Gartner 2001). A reduced leaf area/sapwood area ratio in larger trees has previously been

cited as an adaptation to reduce leaf specific hydraulic resistance in tall trees (McDowell et al. 2002b) or to counteract climatic stress (Maherali and DeLucia 2001). Our study suggests that a reduced leaf area/sapwood volume ratio may also be an adaptation to the hydraulic constraints imposed by increasing tree size that allows greater use of stored water relative to total daily water use. This appears to be inconsistent with a previous finding that, in ponderosa pine, increases in leaf area/sapwood area ratio with increasing tree size serves primarily to improve tree leaf specific hydraulic conductance (Maherali and DeLucia 2001). However, conditions in that study were substantially different from those in our study, including large differences in tree sizes and climate (cf. Maherali and DeLucia 2001). Nevertheless, the relative insensitivity of water storage flux in ponderosa pine to sapwood volume/leaf area ratio (Figure 5) lends support to the conclusion of Maherali and DeLucia (2001) that the primary significance of reduced leaf area/sapwood area ratio with increasing tree size in ponderosa pine is that it improves leaf specific hydraulic conductivity.

In tall trees, we found that the use of stored water was concentrated in morning and early afternoon hours (Figure 1), during times of high solar irradiance. For example, mean above-canopy photosynthetic radiation during withdrawal of stored water in Douglas-fir was $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SD = $510 \mu\text{mol m}^{-2} \text{s}^{-1}$) versus $570 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SD = $370 \mu\text{mol m}^{-2} \text{s}^{-1}$) during daytime storage recharge. Assuming that canopy light declines according to the Beer-Lambert law with a light extinction coefficient of 0.5 (Waring and Running 1998), mean irradiance during withdrawal of stored water would allow photosynthetically saturating radiation of about $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Leverenz 1981) to penetrate twice as deep into the canopy (two leaf area index units) as during recharge. Thus, use of stored water occurs during daytime periods when conditions are most conducive for photosynthesis.

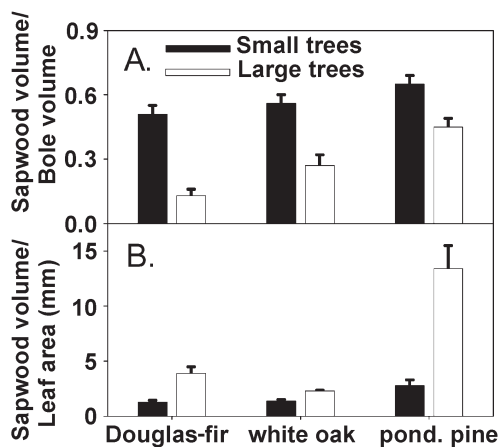


Figure 4. (A) Sapwood volume to bole volume ratios in Douglas-fir, Oregon white oak and ponderosa pine trees ($P < 0.00001$ in all species). (B) Sapwood volume to crown leaf area ratios in Douglas-fir, Oregon white oak and ponderosa pine trees ($P < 0.00001$ in all species).

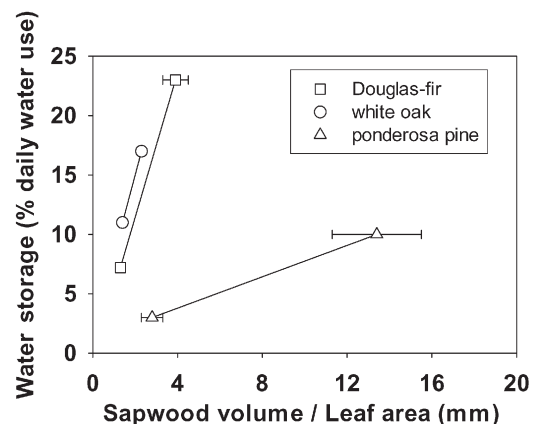


Figure 5. Mean seasonal ratios of daily bole storage flux to daily transpiration flux (vertical axis, %), plotted against sapwood volume to leaf area ratio (horizontal axis, in mm) in Douglas-fir (\square), white oak (\circ) and ponderosa pine (\triangle) trees. Horizontal error bars are standard errors and each symbol indicates a size class.

In Douglas-fir, the differential effect of stored water use on daily photosynthesis with tree size was substantial. Throughout the growing season, use of stored water allowed an average of 18% more photosynthesis to occur in the 60-m tree than if crown flux were constrained to match the time course of bole flux (i.e., 20.0 versus 16.9 mg C s⁻¹). For the three 15-m trees, an average of 10% of diurnal estimated photosynthesis was supported by the use of stored water (1.85 mg versus 1.68 mg C s⁻¹).

The net carbon balance of the old Douglas-fir forest of this study may vary between negative and positive (Harmon et al., unpublished data). Foliage of the old growth trees was estimated to account for over 90% of total ecosystem net assimilation (Harmon et al. 2002). Based on estimates of net ecosystem production and net assimilation of foliage of old growth trees at this site (Harmon et al. 2002), a loss of the 18% of assimilation that we attribute to stored water use, would shift the mean net ecosystem production from slightly positive to negative. However, our small sample size precludes useful inferences about the ecosystem level consequences. Nevertheless, our results show that, at the tree scale, changes in tree water storage with size may compensate to a significant degree for increased path length resistance and gravity (Phillips et al. 2002).

Acknowledgments

This study was funded by the U.S. Department of Agriculture NRI Competitive Grants Program, Contract No. 97-35101-4318, the U.S. Forest Service (Grant No. USDA 97-35101-4376), and the Western Regional Center of the National Institutes for Global Environmental Change. We thank J. Kučera for provision of data, and E. Watrud, N. Gehres, A. Schauer, D. Braun, D. Woodruff and D. Shaw for field assistance.

References

- Becker, P., F.C. Meinzer and S.D. Wullschleger. 2000. Hydraulic limitation of tree height: a critique. *Funct. Ecol.* 14:4–11.
- 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.
- Constantz, J. and F. Murphy. 1990. Monitoring moisture storage in trees using time domain reflectometry. *J. Hydrol.* 119:31–42.
- 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.
- Friend, A.D. 1993. The prediction and physiological significance of tree height. *In* *Vegetation Dynamics and Global Change*. Eds. A.M. Solomon and H.H. Shugart. Chapman and Hall, New York, pp 101–115.
- Goldstein, G., J.L. Andrade, F.C. Meinzer, N.M. Holbrook, J. Cavellier, 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.
- Granier, A. 1985. Une nouvelle méthode pour la mesure de flux de sève brute dans le tronc des arbres. *Ann. Sci. For.* 42:193–200.
- Hinckley, T.M. and D.N. Bruckerhoff. 1975. The effects of a major drought on xylem pressure potential, leaf resistance and stem circumference on a forest-grown white oak (*Quercus alba* L.) in mid-Missouri. *Can. J. Bot.* 53:62–72.
- Hinckley, T.M., J.P. Lassoie and S.W. Running. 1978. Temporal and spatial variations in the water status of forest trees. *For. Sci. Monograph* 20, 72 p.
- 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.
- Hunt, E.R., Jr., S.W. Running and C.A. Federer. 1991. Extrapolating plant water flow resistances and capacitances to regional scales. *Agric. For. Meteorol.* 54:169–195.
- Köstner, B., P. Biron, R. Siegwolf and A. Granier. 1996. Estimates of water flux and canopy conductance of Scots pine at the tree level utilizing different sap flow methods. *Theor. Appl. Clim.* 53: 105–113.
- Kučera, J., J. Čermák and M. Penka. 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol. Plant.* 19:413–420.
- Leverenz, J.W. 1981. Photosynthesis and transpiration in large forest-grown Douglas-fir: diurnal variation. *Can. J. Bot.* 59:349–356.
- Loustau, D., P. Berbigier, P. Roumagnac, C. Arruda-Pacheco, J.S. David, M.I. Ferreira, J.S. Pereira 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.
- Maherali, H. and E.H. DeLucia. 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia* 129:481–491.
- Martin, T.A., K.J. Brown, J. Čermák, R. Ceulemans, J. Kučera, F.C. Meinzer, J.S. Rombold, D.G. 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.
- McDowell, N.G., N. Phillips, C. Lunch, B.J. Bond and M.G. Ryan. 2002a. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiol.* 22:763–774.
- McDowell, N.G., H. Barnard, B.J. Bond et al. 2002b. The relationship between tree height and leaf area:sapwood area ratio. *Oecologia* 132:12–20.
- Morikawa, Y. 1974. Sapflow in *Chaemaecyparis obtusa* in relation to water economy of woody plants. *Tokyo Univ. For. Bull.* 66: 251–257.
- Niklas, K.J. 1994. *Plant allometry*. University of Chicago Press, Chicago, 395 p.
- Pallardy, S.G., J. Čermák, F.W. Ewers, M.R. Kaufmann, W.C. Parker and J.S. Sperry. 1995. Water transport dynamics in trees and stands. *In* *Resource Physiology of Conifers*. Eds. W.K. Smith and T.M. Hinckley. Academic Press, New York, pp 301–389.
- Phillips, N., A. Nagchadhuri, R. Oren and G. Katul. 1997. Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* 11: 412–419.
- Phillips, N.G., B.J. Bond, N.G. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature, and old-growth Douglas-fir trees. *Tree Physiol.* 22:205–211.
- Phillips, N.G., 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.
- Pruyn, M.L., B.L. Gartner and M.E. Harmon. 2002. Respiratory potential in sapwood of old versus young ponderosa pine trees in the Pacific Northwest. *Tree Physiol.* 22:105–116.
- Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and growth. *Bioscience* 47:235–242.
- Ryan, M.G., B.J. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Cienciala and J. Kučera. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia* 124:553–560.

- Schulze, E.D., J. Čermák, R. Matyssek, M. Penka, R. Zimmermann, F. Vasicek, W. Gries and J. Kučera. 1985. Canopy transpiration and water 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.
- Spicer, R. and B.L. Gartner. 2001. Radial and vertical patterns of specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. *Trees* 15:222–229.
- Stewart, C.M. 1967. Moisture content of living trees. *Nature* 214: 138–140.
- Stratton, L., G. Goldstein and F.C. Meinzer. 2000. Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant Cell Environ.* 23:99–106.
- Suchanek, T.H., H. Mooney and J.F. Franklin. 2002. Integrated studies on carbon flux dynamics in an old growth forest. *Ecosystems*. In press.
- Tezara, W., V.J. Mitchell, S.D. Driscoll and D.W. Lawlor. 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature* 401:914–917.
- Tyree, M.T. and S. Yang. 1990. Water storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms: the contribution of capillary water and cavitation. *Planta* 182: 420–426.
- 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 Environ.* 1:131–140.
- Waring, R.H. and S.W. Running. 1998. *Forest Ecosystems: analysis at multiple scales*. 2nd Edn. Academic Press, San Diego, 370 p.
- 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.
- Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40:513–527.
- Zweifel, R., H. Item and R. Häsler. 2001. Link between diurnal stem radius changes and tree water relations. *Tree Physiol.* 21:869–877.