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Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir

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Abstract. Enough water is stored in the sapwood of large Douglas-fir to significantly contribute to transpiration. Sapwood water content falls through the season, causing the wood's conductivity to fall. This leads to low leaf-water potentials, stomatal closure, and reduced photosynthesis by the trees.

The amount of water stored in the sapwood of Douglas-fir 50–60 m tall, growing in the Cascade Mountains of Oregon, was estimated periodically over two seasons from measurements of sapwood relative water content (R_s). The relationship between R_s and volume of water contained in the sapwood was determined in the laboratory, and an equation describing the variation of relative conductivity (K) with R_s was derived from the literature. Stomatal conductance (k_s) and leaf water potentials were measured in the field.

The relative conductivity of the sapwood was calculated from estimates of the flow rate through the tree and differences in water potential between dawn and the time of comparison. Flow rate was assumed to equal transpiration rate, calculated from the Penman-Monteith equation using measured k_s values. A sixfold decrease in K during the summer was attributed to changes in R_s. The maximum observed diurnal variation in K would require a change in R_s estimated at 25%.

About 270 $\mathrm{m^3\ ha^{-1}}$ (27 mm) of water were stored in sapwood, and 75% of that was in the stemwood. Withdrawal from this store reached 1.7 mm $\mathrm{day^{-1}}$ on clear days after cloudy or rainy weather. Recharge could be almost as fast (up to 1.6 mm $\mathrm{day^{-1}}$) after rain, but was very slow if the foliage remained wet.

Introduction

Frictional resistance to water flowing in the roots and stems of plants, together with the gravitational potential in tall trees, substantially reduce pressure in the xylem of rapidly transpiring plants. The relationships between flow and resistance are frequently represented by an Ohm's law analogy (e.g. Richter, 1973), but evidence suggests that in many plants, particularly trees, the analogy breaks down because of capacitance.

The tissues in a plant may be considered as a number of alternative sources of water linked in parallel with each other and the soil (Jarvis, 1975). Thus the total flux from the plant as transpiration (E) may be made up of a number of partial flows within the plant:

$$E = q_1 + q_2 + q_3 \ldots\ldots + q_n \qquad (1)$$

where q_1 is the flow from the soil and q_2 to q_n are flows from storage. The flow from a particular store is:

$$q_i = (\Psi_i - \Psi_{\mathrm{xylem}})/r_i \qquad (2)$$

where r_i is resistance of the tissue to water movement and Ψ_i is a function of the tissue relative water content, R_i. The volume of water that can come from storage is:

$$\Delta V_i = V_i \cdot \Delta R_i = \int_{t_1}^{t_2} q_i \cdot dt \qquad (3)$$

where V_i is the volume of water in the turgid tissue. As Weatherley (1970) pointed out, the relative sizes of the flows out of storage at any one time and their relative phasing depend upon the resistances between the stores and xylem, r_i, the capacity of the stores, V_i, and the relationships between Ψ_i and R_i, the tissue moisture characteristics.

Initially, water will move out of storage from tissue closest to the evaporation sites, the leaves. Because this source is quite small, potential will quickly drop, and the main sources of supply will be progressively lower down the plant (Dobbs & Scott, 1971). If storage within the plant is adequate and the resistances between storage tissue and xylem are lower than between xylem and soil, sufficient water may be withdrawn from tissues to meet transpiration requirements for considerable periods.

When water is withdrawn from wood, cavitation rather than shrinkage occurs (Siau, 1971). In conifer sapwood, numerous bordered pits connect the tangential walls of the conducting tracheary elements to other tracheids. When the water column cavitates, a pressure gradient quickly develops between the affected tracheid and its neighbours. In early wood, a pressure gradient of 0.3 × 10^5 Pa (0.3 bar) will cause bordered pits to close, sealing off gas bubbles from the rest of the conducting tissue (Gregory & Petty, 1973).

Cavitation in conifer tracheids is reversible because it affects only individual conducting elements, not the

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entire conducting column. The time required to recover from cavitation is important for, if recovery takes months, the water stored in the sapwood could make only a small contribution to transpiration. But if cavitation is rapidly reversible, sapwood water could be an important component of transpiration.

When Thomas & Kringstad (1971) dried wood blocks to a moisture content of 4%, the major proportion of pits reopened after soaking the blocks in water for only 1 week. Field studies of seasonal changes in sapwood relative to water content (R_s) in Great Britain (Chalk & Bigg, 1956) and in Canada (Clark & Gibbs, 1957) suggest rapid rates of withdrawal and low recharge of the sapwood in a variety of conifers including Douglas-fir.

The aim of this study was to assess variation in the rate of withdrawal and recharge from the sapwood of old-growth Douglas-fir in the Pacific Northwest of North America. There winters are wet but rarely freezing, and summers are consistently dry; consequently, rates of sapwood water depletion and resaturation should be high. Further, by measuring shoot water potential and transpiration rate diurnally when the sapwood has different relative water contents, we sought to evaluate to what extent cavitation affects stem conductance.

Study area

Because the necessary biomass and climatic data were readily available, we selected Coniferous Forest Biome Reference Stand 17 in the H. J. Andrews Experimental Forest, an International Biological Programme site situated 70 km east of Eugene, Oregon, in the west-central Cascade Mountains (latitude 44° N, longitude 122° W).

The research stand was dominated by Douglas-fir (*Pseudotsuga menziesii*) trees, 50–60 m tall with diameters up to 1.5 m at 1.3 m above ground. Most wood volume was contributed by the overstory Douglas-fir; the understory canopy was western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Biomass and water storage for the major structural components of the Douglas-fir in this stand are estimated in Table 1.

Note that mean monthly temperatures (Fig. 1) remained above freezing during the study period, even in December and January. Less than 5% of the 2454 mm of precipitation from July 1, 1975 to July 1, 1976 fell during the summer. The patterns of precipitation and temperature clearly indicate that the growing season from May through September was a time of high potential evaporation; transpiration was generally low during winter.

Table 1. Biomass and water storage in old-growth Douglas-fir

Component	Dry weight* ($t\ ha^{-1}$)	Density ($g\ cm^{-3}$)	Total volume ($m^3\ ha^{-1}$)	Sapwood fraction	Sapwood volume ($m^3\ ha^{-1}$)	Available water fraction	Available water volume ($m^3\ ha^{-1}$)
Foliage	9.9	1.00	1.5	–	–	0.20	0.3
Living branches	36.7	0.60	61.2	0.50	30.6	0.49	15.0
Stem wood	604.5	0.45	1343.3	0.26	349.3	0.57	199.0
Roots > 5 mm dia.	140.0	0.45	311.1	0.30	93.3	0.57	53.2
Totals	791.1		1717.1		473.2		267.5

* From Grier & Logan (1977).

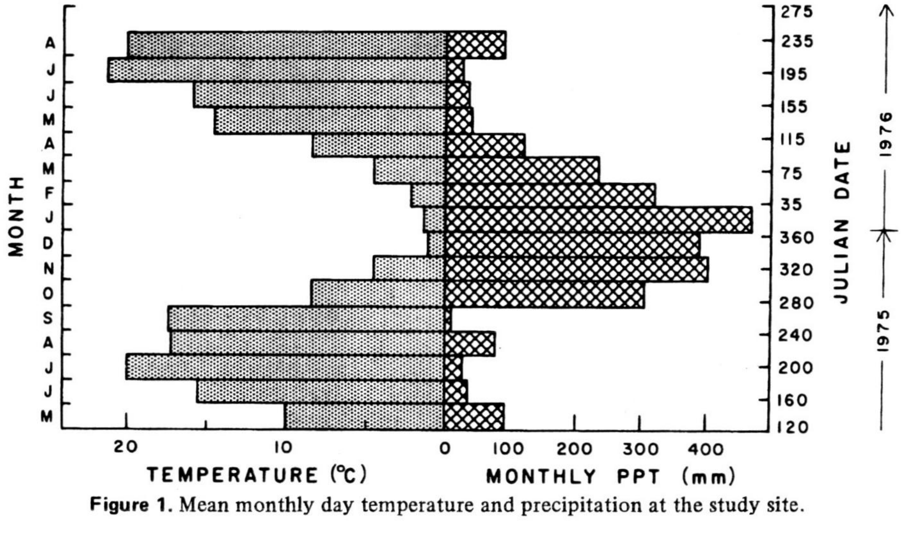

Figure 1. Mean monthly day temperature and precipitation at the study site.

Methods

Transpiration rate (E)

Throughout selected summer days when the trees had different sapwood relative water contents (R_s), the rate of transpiration from the canopy was estimated hourly using the Penman-Monteith combination equation (Monteith, 1965).

Based on studies of evaporation from Scots pine forests in England (personal communication with J. B. Stewart, Institute of Hydrology, Wallingford, Oxon, England), the canopy was assumed wet when the vapour pressure deficit remained below 100 Pa (1 mb). Thus transpiration, as distinct from evaporation, was estimated using appropriate values of stomatal conductance (k_s) when the vapour pressure deficit (D) was larger than 100 Pa (1 mb). We assumed that the average values of k_s for samples of foliage at a height of 40–45 m represented the entire canopy. The necessary climatic data were available from a central meteorological station where air temperature, dew point temperature, shortwave incoming radiation, and wind speed were averaged hourly (Waring, Holbo, Bueb, & Fredriksen, 1978). Net radiation in the canopy was calculated as 0.8 of the shortwave radiation (after Gay, 1971).

Evaporation from wet canopies was estimated from equation (4) with infinite k_s. Because boundary layer conductance (k_a) is large relative to k_s for conifer needles, even at low windspeeds, the rate of transpiration rarely exceeds 5% of the evaporation rate of free water from the leaf surfaces (Jarvis, James, & Landsberg, 1976). Thus, to provide a closer comparison with actual transpiration, a reference rate of potential transpiration was also calculated with k_s set to the maximum measured value of 0.2×10^{-2} m s^{-1} expressed on the basis of total surface area (Running, 1976).

Leaf stomatal conductance (k_s)

Foliage was sampled on 3 days from 3 trees at a height of 40–45 m. A 12-gauge shotgun loaded with 00 buckshot was used to remove samples of shoots. Shoots were caught and immediately placed in a null-balance diffusion porometer to measure leaf conductance (Beardsell, Jarvis, & Davidson, 1972).

The shoots, stored in plastic bags, were taken to the laboratory where a surface area meter (Lambda Instruments, Inc.) determined projected leaf area. Leaf conductance was calculated from leaf area, balancing flow rates, temperature, and humidity within the porometer chamber (Beardsell *et al.*, 1972). Results were expressed on a total surface area basis, 2.5 times the projected leaf area.

Leaf water potential (Ψ_L)

Leaf water potential was measured with a pressure chamber (Scholander, Hammel, Bradstreet, & Hemmingsen, 1965) on shoots sampled simultaneously for leaf conductance measurements. In addition, some shoots from the trees were sampled at night for estimating maximum water potential at the time of minimum transpiration.

Sapwood relative water content (R_s)

The relative water content of sapwood (R_s), expressed as a percentage, was calculated from:

$$R_s = \frac{W_f - W_d}{V_f - V_s} \cdot 100 \tag{4}$$

where W_f = fresh weight of wood, g; W_d = dry weight of the wood, g; V_f = volume of the wood, cm^3; V_s = volume of solid material in the wood (= $W_d/1.53$), cm^3.

The volume of solid material was calculated from the dry weight assuming that cellulose and lignin had a constant density of 1.53 g cm^{-3} (Siau, 1971; Skaar, 1972). Sapwood water deficit was ($100 - R_s$).

R_s was measured on wood cores from five to ten large Douglas-fir sampled weekly throughout the summer and at somewhat longer intervals during the rest of the year. The cores, from the outer 2-cm band of sapwood at 1.3-m height, were collected with an increment borer. Two cores with a total volume of 0.6079 cm^3 were taken from each tree, placed in vials, and later transported to the laboratory to be weighed, dried at 70°C, and reweighed.

To check the uniformity of R_s within individual trees, it was measured at various positions on nine trees 25- to 30-m tall immediately after they had been felled. Some trees had virtually no variation, as found by Chalk & Bigg (1956) and Clark & Gibbs (1951), but at other sampling times the values from the upper portion of trees were 10–15% different from those at 1.3 m. Across the sapwood at the same height, we found only about a 5% variation, similar to that reported by Chalk & Bigg (1956) in Douglas-fir.

Limited sampling in August, September and October failed to show a significant diurnal variation in R_s. For making comparisons throughout the year, we always tried to sample between 0800 and 1000 h.

Sapwood relative conductivity (K)

In the xylem, liquid water moves by masss flow along gradients of hydrostatic pressure (P) in the absence of membranes so that xylem pressure potential is the appropriate driving force. Movement into cells adjacent to the pathway is by osmosis across membranes along gradients of water potential (Ψ). Because Ψ is in dynamic equilibrium with xylem pressure potential and because the osmotic potential of xylem sap is small, we may assume that $\Psi = P$ at a given height (Jarvis, 1975). Thus, the flow at any point is:

$$q = K \int_{z_2}^{z_1} \frac{d\Psi}{dz} dz = (\Psi_1 - \Psi_2)K \tag{5}$$

where $(\Psi_1 - \Psi_2)$ is the pressure drop or water potential difference between z_1 and z_2 (Pa). Included in the sapwood relative conductivity, K, are effects attributable to the length and cross-sectional area of the pathway and the viscosity of water which depends on both temperature and solute (Heine, 1971). Specifically, K, with units of m^2, is defined:

$$K = \frac{q \eta l}{A_s (\Psi_1 - \Psi_2)} \tag{6}$$

where η = the viscosity of xylem sap, N s m^{-2}; q = the flow rate, m^3 s^{-1}; l = the path length, m; A_s = the cross-sectional area of sapwood, m^2.

Average K values for a tree were calculated with equation (6) assuming: water potential follows a uniform gradient from the base of the tree to the crown; transpiration (E) approximates flow rate (q); the appropriate area (A_s) equals the average of that at 1.3 m and at the base of the crown; and the xylem sap is pure water with a viscosity dependent upon ambient temperature. We assume that the relative conductivity can be calculated at a specified height (40–45 m) by comparing the difference in leaf water potential at predawn, when $q \simeq 0$, with the water potential when transpiration is occurring.

An alternative calculation, which does not include the effects of viscosity, is defined as conductivity, G, with units of m^5 N^{-1} s^{-1} (Heine, 1971).

Volume of available water (ϕ_a)

In a sample of wood of volume (V_f) at saturation, the volume of water (V_{H_2O}) is:

$$V_{H_2O} = V_f - V_s = V_f - \frac{W_d}{1.53} \tag{7}$$

as defined in equation (4).

The specific gravity ($S.G.$) of the sample is:

$$\text{S.G.} = \frac{W_d}{V_f}$$

Substituting for W_d into equation (7):

$$V_{H_2O} = V_f \left(1 - \frac{\text{S.G.}}{1.53}\right)$$

Dividing through by V_f, the volume fraction occupied by water (ϕ) is:

$$\phi = 1 - \frac{\text{S.G.}}{1.53}$$

Specific gravity, determined from core samples, decreased from 0.5 at the base to 0.3 at the crown of rapidly growing Douglas-fir 30-m tall. Assuming a conservative average value of 0.45,

$$\phi = 0.71 \text{ (m}^3\text{ of water per m}^3\text{ of wood).}$$

To determine the fraction of ϕ available for exchange, uniform samples of saturated Douglas-fir sapwood were cut into 5.4 cm^3 discs and placed above salt solutions of different osmotic potentials (π) for 6 weeks to equilibrate to constant weight. R_s was calculated from equation (4). Once cavitation occurred, a water potential of only -10×10^5 Pa (-10 bar) was required to remove 80% of the water from the sapwood (Fig. 2). The water bound in hydration with the cell walls was estimated to be somewhat less than 20% of the saturated content. Other calculations (after Siau, 1971) yield a similar value; therefore, up to 80% of the water in saturated sapwood was assumed available. Thus, the volume fraction of available water was:

$$\phi_a = 0.8\,\phi = 0.57$$

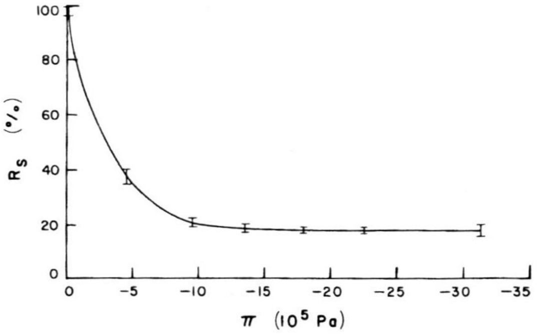

Figure 2. The relation between relative water content (R_S) of Douglas-fir sapwood and water potential. Discs of wood (5.4 cm^3) were equilibrated over NaCl solutions with a range of osmotic potentials (π) for 6 weeks. Standard errors are indicated by vertical lines.

The sapwood volume of the stem was estimated using the linear relationship that Grier & Waring (1974) determined between foliage weight and sapwood cross-sectional area at a height of 1.3 m. The foliage biomass of 9.9 t ha^{-1} corresponds to a sapwood basal area of 13.42 m^2 ha^{-1}. Our observations on smaller trees suggest that sapwood area decreases 50% between 1.3 m and the base of the crown. Assuming the base of the crown is at an average height of 35 m, the volume of sapwood below the crown (V_{sw}) is:

$$V_{sw} = \left[\frac{13.4 + (0.5)\,13.4}{2}\right] \cdot 35 = 349 \text{ m}^3\text{ ha}^{-1}$$

This figure is 26% of the total volume of stemwood, again a conservative estimate for total volume of sapwood because most of the stemwood in the crown is also sapwood. Then the volume of available water is:

$$V_a = V_{sw} \cdot \phi_a = 349 \cdot 0.57 = 199 \text{ m}^3\text{ ha}^{-1} \text{ (20 mm of water).}$$

The sapwood fraction of living branches and roots was conservatively estimated from a few samples, and available water was similarly estimated (Table 1).

For the foliage, the maximum change in R_L was assumed to be 20% over a range in Ψ_l from 0 to -30×10^5 Pa, and the saturated weight was assumed equivalent to 150% of the dry weight, so the maximum volume of water stored in the foliage was 0.3 m^3 ha^{-1} (0.03 mm of water).

Thus, the stemwood contains at least 75% of the total water stored in the trees, and a 1% change in R_s represents 2.5 m^3 ha^{-1} (0.25 mm) of water. For the tree as a whole, a 1% change in R_s is equivalent to 3.3 m^3 ha^{-1} (0.33 mm) of water. The foliage stores only 0.1% of the total capacity (see Table 1).

Results

Seasonal variation in sapwood water deficit and potential transpiration

Average values of potential transpiration (that is, with $k_s = 0.2 \times 10^{-2}$ m s^{-1}) for 5-day periods are shown in Fig. 3 with corresponding changes in sapwood water deficit.

R_s changed most rapidly after rain during summer. For example, R_s increased from 48 ± 2% after 12.5 mm of precipitation on days 191-192 to 77 ± 5% on day 198 (± figures are standard errors). From our estimates of water storage (Table 1), such a change in stem sapwood alone represents 72 m^3 ha^{-1} or 7.2 mm of water. On a daily basis, this is a net increase of 1.2 mm day^{-1}. R_s also changed rapidly between days 234 and 243 when only 3 days were dry, and a total of 43.1 mm of precipitation fell. Then R_s increased from 57 ± 4% to 76 ± 3% or 0.5 mm day^{-1}.

The most rapid decrease in R_s was measured immediately after days 243-247 when no precipitation fell and potential transpiration was high ($>$ 10 mm day^{-1}). During these 4 days, R_s declined from 76 ± 3% to 56 ± 2%, indicating that the stemwood was supplying 1.25 mm day^{-1} and the total sapwood contributed 1.7 mm day^{-1}.

During October, more than 300 mm of rain were recorded (Fig. 1), yet R_s rose by only 14% from September 26 (day 269) to October 30 (day 303). However, potential transpiration during this period also fell to below 1 mm day^{-1}, and the foliage was completely dry for only 2 days.

Throughout the autumn and early winter, R_s continued to rise at a slow but nearly constant rate of 0.33% day^{-1}.

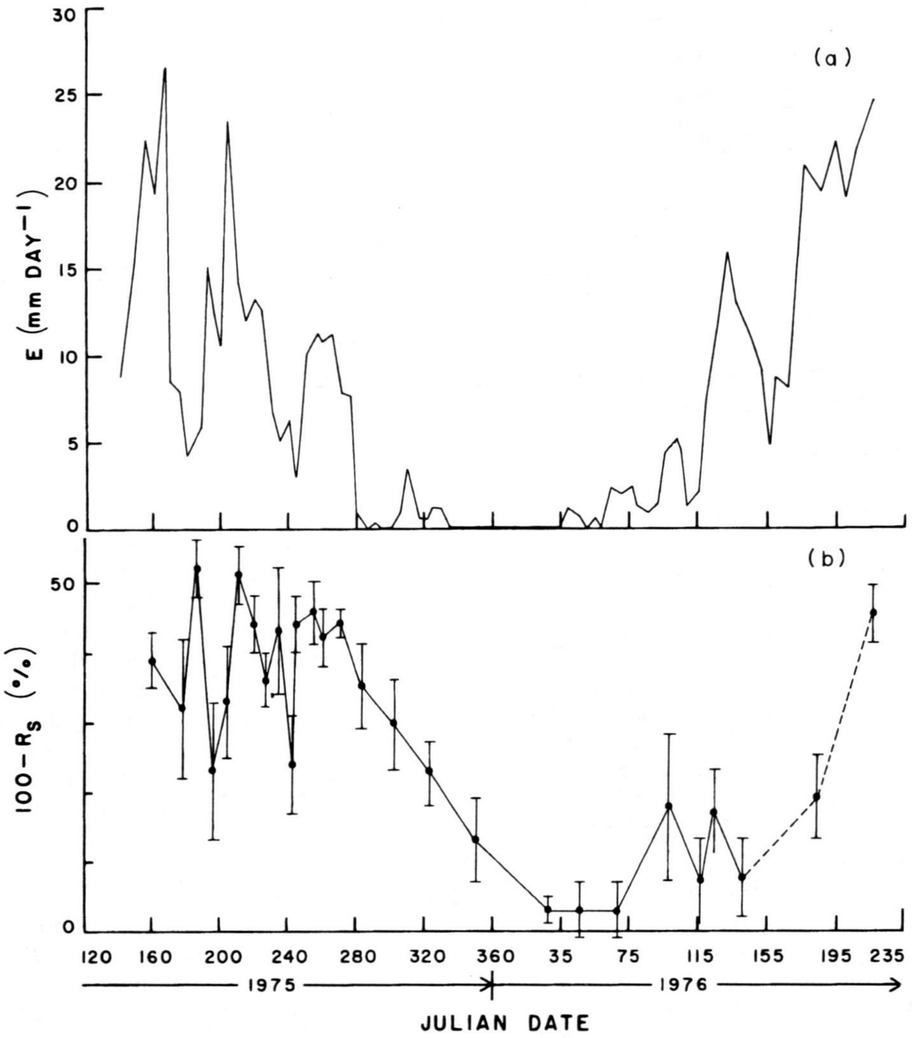

Figure 3. Relationship between potential transpiration (E) and sapwood water deficit (100-R_s) in Douglas-fir. (a) Potential transpiration from the canopy with a leaf area index of 8.4 (total leaf area of 20.2), averaged for 5 days previous to date plotted. Values calculated with Penman-Monteith equation assuming a constant k_s of 0.20 × 10^{-2} m s^{-1} and windspeed of 1 m s^{-1}. (b) Sapwood water deficit shown through a cycle of depletion and recharge. Values determined from 0.6079 cm^3 cores taken at 1.3-m height on five to ten trees. Standard errors are indicated by vertical lines.

After a period of 57 days without dry foliage, the sapwood reached full capacity by January 23 and remained saturated until day 69; R_s subsequently varied between 82 and 93% until the end of May (day 139). Thereafter, we greatly reduced our sampling intensity, and we may only conclude that a major deficit in sapwood water content again developed in August 1976.

Comparing *E* with sapwood water deficit (Fig. 3) shows that sapwood did not remain at full capacity if potential transpiration exceeded 4 mm day^{-1} for a 5-day period.

Diurnal variation in transpiration and leaf water potential

Examples of diurnal variation in leaf stomatal conductance (k_s) and shoot water potential (Ψ_L) are shown in Fig. 4. The selected day–May 6, 1976 (day 127)–was in the first week of the growing season. Even with adequate soil water, k_s fell from 0.15 to 0.05 × 10^{-2} m s^{-1}, or more than 70% between 08.30 and 12.00 h. Water potential dropped from -7.5 to -19.2×10^5 Pa during the same period. Vapour pressure deficit, *D*, reached a maximum of 190 Pa (19.0 mb) at 1400 h, closely following changes in air temperature. R_s measured on three trees averaged 90% at 0800 h.

Similarly, we compared 2 other days. 1 July 1976 (day 183) was also clear but had a notable delay in the development of maximum *D*. This resulted in k_s falling more slowly from 0.1 to 0.03 × 10^{-2} m s^{-1}. Shoot water potentials also fell less rapidly from -6.1 at dawn to -18.1×10^5 Pa in the late afternoon when *D* reached 191 Pa (19.1 mb). Average R_s at the start of the day was 78%. 4 September 1975 (day 247) was also clear with predawn Ψ_L of -9.0 and a minimum Ψ_L of -23×10^5 Pa. Average R_s was 56%, and k_s fell from 0.07 to 0.01 × 10^{-2} m s^{-1} at 1400 h when *D* reached 220 Pa (22.0 mb).

The diurnal course of actual transpiration (E) increased until 1000 h on May 6 and July 1 and until 1200 h on September 4. The total amount of water transpired on each of the 3 days was 3.5, 3.1, and 1.8 mm day^{-1}.

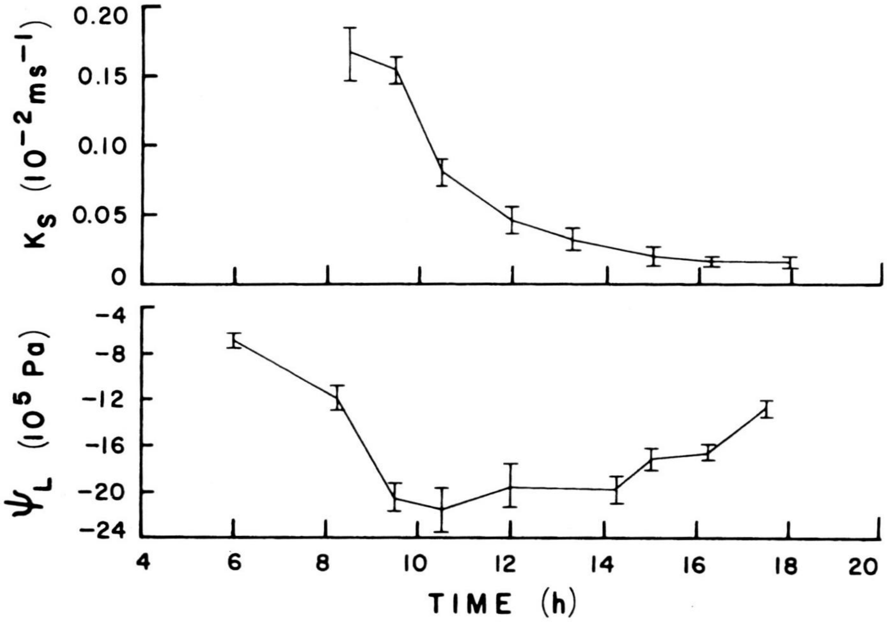

Figure 4. Diurnal variation in stomatal conductance (k_s) and leaf water potential (Ψ_L) on 6 May 1976. Standard errors are indicated by vertical lines.

Comparing Ψ_L with *E* at intervals throughout the 3 summer days reveals different patterns (Fig. 5). Ψ_L was much higher in the morning than in the afternoon on 6 May when R_s initially was 90%. Less difference was apparent on 1 July when R_s was initially 78%, and none was evident on 4 September when R_s was initially only 56%. The reduction in Ψ_L with increasing *E* became more pronounced as R_s decreased. Compared to the morning of 6 May, the pressure drop required to supply the same rate of transpiration was 2.3 and 6.3 times larger on the mornings of 1 July and 4 September.

Diurnal variation in relative conductivity (K)

The diurnal changes in both stem conductance (*G*) and relative conductivity (*K*) follow similar general trends (Fig. 6), but inclusion of the temperature-dependent viscosity in calculating *K* tends to reduce diurnal variation. Values of *G* and *K* were highest on the morning of May 6 when R_s was 90%. Values were similar throughout May 6 and July 1 (initial R_s of 90% and 78%), but they were much less on September 4 (initial R_s of 56%).

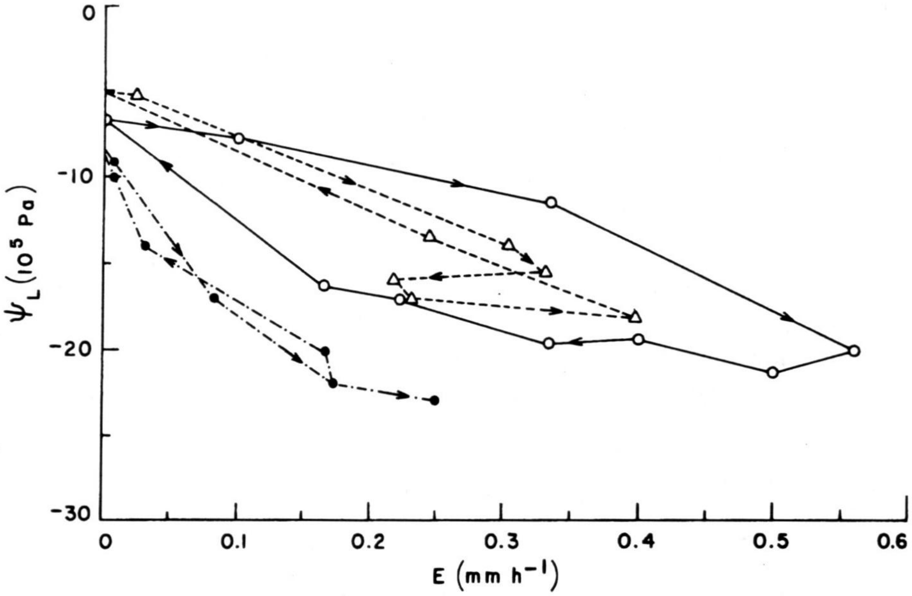

Figure 5. Leaf water potential (Ψ_L) in relation to transpiration (E) on days with different relative water contents in sapwood (R_s). Arrows indicate the course of time. Each point is the average from three trees.

Date	R_s	E (mm day^{-1})
(○) May 6, 1976	90	3.5
(△) July 1, 1976	78	3.1
(●) Sept. 4, 1975	56	1.8

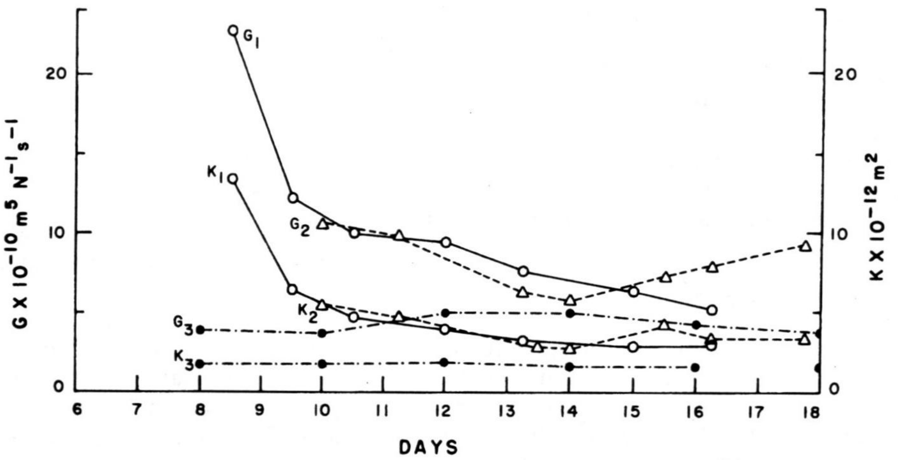

Figure 6. Diurnal variation in stem conductance (G) and relative conductivity (K) on the same 3 days.

Date	R_s
(○) May 6, 1976	90
(△) July 1, 1976	78
(●) Sept. 4, 1975	56

Discussion

The seasonal analysis of R_s suggests that contributions of water from that stored in sapwood are largest in the spring and early summer. Depletion of sapwood water began almost as soon as transpiration, consistent with the hypothesis that the most readily available sources of water are drawn on first (Weatherley, 1970).

The rate of change in R_s did not exceed 5% day^{-1} and fell to as little as 0.33% day^{-1} during the period of winter recharge. Because all sampling was restricted to the outer 2-cm band of sapwood near the base of the tree, larger changes possibly occurred higher up, particularly in the canopy where specific gravity of the wood is less and the water potentials are lower.

The amount of water contributed from sapwood in the stem reached 1.2 mm day^{-1}. If all the sapwood in the tree contributes similarly, the total contribution could reach 1.7 mm day^{-1}. However, the limbs with their higher wood density are less likely to suffer cavitation and probably do not contribute as much. The roots, nearest the water in the soil and furthest from the demand, probably contribute in a minor way too.

The seasonal variation in R_s (Fig. 3) is similar to the findings of Chalk & Bigg (1956) and Clark & Gibbs (1957).

Although the foliage was fully rehydrated by October 3, R_s remained low until well into November, then rose steadily until the stem was completely recharged in mid-January. Apparently numerous cavitated tracheids cannot refill instantly when transpiration is very low, but instead refill gradually over an extended period.

The relative conductivity of sapwood varies linearly with wood S.G. (Gregory, 1972). As S.G. decreases, the actual conducting area increases proportionately. More importantly, as Puritch (1971) has demonstrated in carefully designed laboratory experiments, the relative conductivity of sapwood of a given S.G. decreases exponentially as R_s decreases. We have attempted to generalize Puritch's findings on both outer and inner sapwood from *Abies grandis* by normalizing the values to predict $\hat{K}$ as a percentage of the value of K at a relative water content of 100% in sapwood (Fig. 7). The relationship can be described by:

$$\hat{K} = 0.4092e^{0.055R_s}\,(\%) \qquad (8)$$

This relationship indicates that a decrease in R_s from 100% to 90% can reduce $\hat{K}$ to 58% of that at saturation, whereas a reduction in R_s from 70% to 60% represents a decrease in $\hat{K}$ from 19% to 11%. As R_s is reduced to the bound water level around 20%, K approaches 0.

Such an exponential relationship is to be expected as a result of the pore size distribution. The first conducting elements to cavitate will be those of largest diameter (for example, Byrne, Begg & Hansen, 1977). The larger diameter tracheids, common to the low S.G. wood laid down in the spring, conduct much more efficiently. On the other hand, the denser, later wood—while much less efficient—is also less likely to cavitate (Gregory & Petty, 1973).

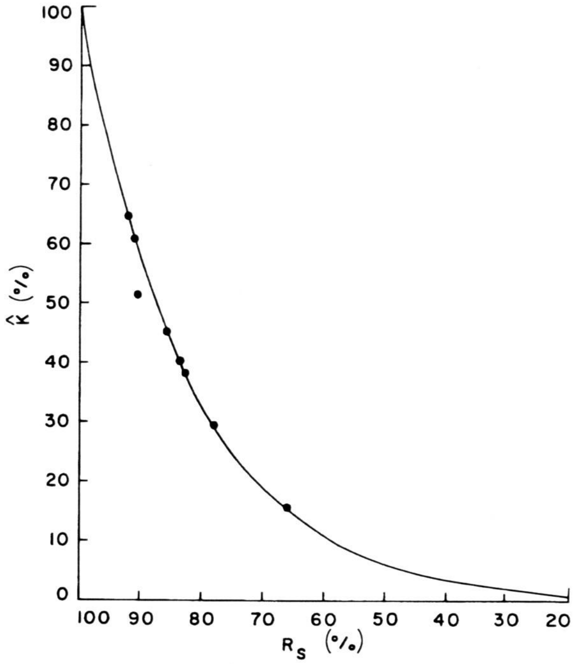

Figure 7. The relation between sapwood relative conductivity, $\hat{K}$, and sapwood relative water content, R_s, for *Abies grandis*. The points are mean values taken from Puritch (1971). Relative conductivity, K, has been normalized with respect to the relative conductivity of saturated sapwood (i.e. that at $R_s = 100\%$) to give $\hat{K}$. $\%\hat{K} = 0.4092e^{0.055(R_s\,\%)}$; $r^2 = 0.97$.

By comparison with the morning of 6 May, K had decreased by a factor of 2 on the morning of July 1 and a factor of 6 on September 2. Based on these reductions, concomitant values of R_s, $\hat{R}_s$, can be predicted from Fig. 7. Measured R_s and $\hat{R}_s$ predicted in this way agreed extremely well:

	R_s (%)	$\hat{R}_s$ (%)
1 July	78	75
4 September	57	56

Thus, from applying Puritch's findings, the seasonal reductions in K can be attributed directly to the seasonal fall in R_s.

Considering diurnal changes in transpiration rate, water potential, stomatal conductance, and relative conductivity, evaluating diurnal variation in R_s at the same time would have been highly desirable, but this was not done. However, probable diurnal changes in R_s can be roughly estimated from the measured diurnal changes in K and further application of equation (8).

On the morning of May 6 with R_s initially at 90%, K was 13.4×10^{-12} m^2. During the afternoon of the same day, K dropped to 3.0×10^{-12} m^2, corresponding to a change in $\hat{K}$ of 58% to 13% of that at saturation or a reduction from the initial value of more than 75%. Fig. 7 shows that this equals an average decrease in R_s of 25%.

On July 1, the initial value of K was only 41% of that on the morning of 6 May. Between 1000 and 1400 h,

K decreased from 5.5 to 2.7×10^{-12} m^2 and, thereafter, increased again reaching 4.4×10^{-12} m^2 in the late afternoon. This change in K corresponds to a fall in R_s from 78% to a minimum of 65%. In September the initial value of R_s was only 56%, and K was much lower and much less variable, ranging from 1.7 to 2.0×10^{-12} m^2. Average $\hat{K}$ was 9%, and the calculated diurnal variation in R_s was less than 3%.

Recently the senior author measured R_s of Scots pine 3- to 5-m tall through the first clear days of the growing season immediately after snow melt in Sweden (23–24 May 1977). In these small trees, R_s changed 20% from 81% to 61% (standard error = 2%) during a day similar in several respects to May 6 in this study. Thus, on May 6, the R_s of Douglas-fir quite possibly could have changed diurnally by 25%.

The marked hysteresis in the relation between Ψ_L and E at high R_s on May 6 and the lack of hysteresis at low R_s on September 4 are consistent with the hypothesis that water moves to the evaporation sites in the leaves from the nearest sources of most readily available water, such as the branches and sapwood in the tree crown (Jarvis, 1976). R_s is unlikely to have changed uniformly throughout the tree. Rather we expect that the R_s of sapwood in the upper crown may be higher at the start of the day and that a large change in R_s in that part of the tree could account for much of the change in K. We have found the crown wood on smaller trees (30-m tall) to have a R_s of 90% to 95%, while the stemwood below was at 80% to 85%.

Because these tissues are finite sources of water, their capacity to supply water must decrease as water is withdrawn. Thus, as transpiration increases through the morning, sapwood water deficit is likely to spread down the tree, progressively reducing average K. As transpiration falls again in the afternoon, this process would be expected to reverse and K to increase again as on July 1, provided that water is available in the soil and that K is high enough for the water to move easily through the plant. However, as the season progresses and the store of water in the sapwood empties, K falls further and remains low, possibly because it is now too low for water to move easily back into the large number of cavitated tracheids.

Once R_s reaches an extremely low level in the autumn, the sapwood probably cannot provide a substantial supply of water for transpiration (cf. Roberts, 1976). However, in the summer when R_s is changing substantially from day to day and probably also diurnally, large amounts of water from the sapwood may be transpired. For example, depletion of stored water on 6 May is calculated as more than 6 mm, much higher than our calculated E. However, allowing for errors in biomass estimates and in our assumptions and measurements of leaf stomatal area, as well as allowing for the fact that even a generalized relationship as defined for *Abies grandis* is unlikely to exactly fit old-growth Douglas-fir trees, sapwood clearly stores a considerable amount of water that is drawn upon to meet the evaporative demand.

Notwithstanding this supply of water, stomatal conductance falls almost from the onset of appreciable transpiration in April until October, possibly because Douglas-fir stomata respond to a saturation deficit (Tan & Black, 1976).

Our data suggest that large trees may be particularly sensitive to high evaporative demand as evidenced by almost complete stomatal closure in the afternoon during the first week of the growing season. Because stomatal conductance affects photosynthesis as well as transpiration, the results strongly support the conclusion reached by Emmingham & Waring (1976) that Douglas-fir trees in the Pacific Northwest may accumulate more than 50% of their total assimilation from October to May.

Summary

Sapwood is a major reservoir for water. In old-growth Douglas-fir, it may be drawn upon to supply 1.7 mm day^{-1} for short periods. During the summer, recharge at the rate of 1.0 mm day^{-1} is not uncommon after precipitation. During autumn and winter when the canopy is wet much of the time, recharge averages less than 0.1 mm day^{-1}. The total storage capacity of the Douglas-fir forest is estimated at 267 m^3 water ha^{-1} (26.7 mm), 75% of which is in the stemwood.

Stem conductance (G) and relative conductivity (K) decrease more than sixfold between May and September, signifying that a proportional increase in pressure drop ($\Delta\Psi$) is required to maintain the same transpiration rate. These changes can be accounted for by an exponential decrease in G and K expected from measured changes in sapwood relative water content (R_s).

Calculations suggest that, under some conditions, a diurnal change in R_s of as much as 25% may be required to explain the observed decrease in G and K. Although R_s in small trees changed 20%, a much smaller overall change can be expected in large trees. The largest variation is likely in the upper stem and crown where R_s may be initially higher than at the base of the tree and where the specific gravity of wood is notably less.

The fact that large trees begin to deplete their sapwood water reservoirs and to close their stomata almost from the onset of transpiration in April supports other studies that indicate October to May as a critically important period for the carbon balance of conifers in the Pacific Northwest of the United States.

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