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The contribution of stored water to transpiration in Scots pine

R. H. WARING*, D. WHITEHEAD† & P. G. JARVIS‡ * School of Forestry, Oregon State University, Corvallis, Oregon 97331, U.S.A., † Forest Research Institute, Rotorua, New Zealand and ‡ Department of Forestry and Natural Resources, University of Edinburgh, King's Buildings, Mayfield Road, Edinburgh EH9 3JU, U.K.

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Abstract. The amount of water available diurnally and annually from the storage tissues was measured in plots of Scots pine trees with four different population densities (608–3281 trees per ha) in a 40-year-old plantation in north eastern Scotland. The water storage capacity of stems, branches, and foliage was estimated from equations derived from harvested trees and measurements of relative water content. On average 64% of the water considered to be available for transpiration was in the stem sapwood and less than 5% in the phloem, cambium and foliage. Trees on the plot with the highest population density had a water storage capacity of 212 m^3 ha^{-1} (21.2 mm), whereas those on the plot with the lowest population density had a water storage capacity of 124 m^3 ha^{-1} (12.4 mm). The utilization of stored water in transpiration was estimated from seasonal and diurnal measurements of the relative water content of foliage and stem sapwood. The largest change in sapwood relative water content over a 2-week period was a reduction of 27% corresponding to extraction from the sapwood of 2.5 and 5.1 mm of water on the plots with the lowest and highest population densities, respectively. In rapidly changing weather conditions 1–1.5 mm day^{-1} could be removed from the stem sapwood alone. Since transpiration rarely exceeded 3 mm day^{-1}, 30–50% of the transpired water was extracted from water stored in the stem sapwood over short periods. Trees on the plot with the lowest population density occasionally had slightly higher relative water contents and exhibited larger diurnal fluctuations than those on the plot with the highest population density, possibly because of differences in wood density. Sapwood water content was generally lower at times of high transpiration rate and in winter during freezing conditions. Resaturation took several months to complete during the winter.

Introduction

When water evaporates from leaves, the water potential of leaf cells is reduced and water moves upwards through the tree along the potential gradients established. The rate of movement through the tree depends on the size of the potential gradient from roots to leaves and on the resistances in the pathways. However, not all water movement is through-flow since trees have a substantial capacity to store water which may be withdrawn from storage as transpiration rates or resistance to withdrawal from the soil increases and the potential in the conducting tissue falls (Jarvis, 1975). Changes in stored water content with changes in potential have been examined in apple trees by Landsberg, Blanchard & Warrit (1976) and such changes should be included in models of water movement in trees.

On the basis of seasonal measurements of sapwood water content, Waring & Running (1978) suggested that the sapwood in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) serves as a major reservoir of water. In contrast, however, Roberts (1976) concluded that water stored in the sapwood contributed little to transpiration in trees of Scots pine (*Pinus sylvestris* L.) which had been severed from their roots. The trees in these two studies differed considerably with respect to age, size and environment, but we would expect the processes affecting storage and water transport to be similar. One of the major objectives of the present study was to determine whether water stored in the sapwood does serve as a significant reservoir of water for transpiration and how to resolve these contrasting results. We have therefore measured the quantities of water available diurnally and annually from storage tissues of Scots pine and their significance to the water balance of the trees.

Materials and methods

Site

In 1936 Roseisle Forest was planted by the Forestry Commission on fine, blown sand 9 m above sea level on the Moray Firth in northeastern Scotland (latitude 58° N, longitude 4° W, National Grid Ref. NJ 664 116). The work described in this paper was done in this forest in 1977 on stands of Scots pine managed to have

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tree spacing ranging from 0.9 to 2.4 m (see Whitehead 1978).

Meteorological measurements

Global and net radiation, wet and dry bulb air temperatures, wind speed and direction, as well as rainfall, were measured at 5 min intervals and recorded on magnetic tapes by an automatic weather station (Strangeways, 1972) on a tower 5 m above the canopy on Plot 2. Tapes and batteries were replaced fortnightly.

Hourly means and totals of the meteorological variables were computed at the Institute of Hydrology, Wallingford. Transpiration from the canopy was estimated using the Penman–Monteith equation (Monteith, 1965) assuming that surface conductance of the canopy, when no intercepted water was present, fell from a maximum of 1 cm s^{-1} in the morning to a minimum of 0.3 cm s^{-1} in the late afternoon (Gash & Stewart, 1977). During or after rainfall, when the vapour pressure deficit of the air was less than 0.1 kPa, it was assumed that the canopy was wet and evaporation was calculated assuming infinite stomatal conductance (Stewart, 1977).

Tree dimensions

The tree dimensions and canopy characteristics were determined by destructive harvesting of three trees on each plot (Whitehead, 1978) and are presented in Table 1. Branch weight was estimated by regression on tree diameter at 1.3 m above the ground using equations provided by M. T. Lim & J. E. Cousens (personal communication); root weight was similarly estimated using equations given by Albrektsson (1976) and Miller & Miller (1976). The thickness of phloem and cambium was measured at 1.3 m, and assumed constant to a height of 10 m. The total volume and weight of each tissue on each plot was calculated by summing the estimates for the amount of tissue for every tree across the range of diameter classes.

Changes in water content

Foliage. Diurnal changes in foliage water content were measured on samples of ten needles from at least two trees in the canopies of Plots 1 and 2. After collection the needles were immediately cut to a length of 2 cm and stored in air-tight glass vials until evening, when fresh weights were measured. To determine relative water content the needles were brought to full turgor by placing the cut ends in water at 5°C for 24 h. They were then carefully blotted between filter papers for 30 s under a 500 g weight, weighed, oven-dried at 80°C, and reweighed (Jarvis & Jarvis, 1963). Relative water content of the needles (R_l) was calculated from (Weatherley, 1950):

$$R_l = \frac{W_{fl} - W_{dl}}{W_{tl} - W_{dl}} \cdot 100 \qquad (1)$$

where W_{fl}, W_{dl} and W_{tl} are the fresh, dry, and turgid weights of the leaves, respectively.

The storage capacity of the foliage, or the maximum amount of water which can be considered to be available for transpiration ('available' water) was calculated from the difference between the relative water content of needles sampled at dawn and that of water-stressed needles on severed twigs, ΔR_l, and the volume of water in the foliage of the stand, V_{wl}, as $\Delta R_l \times V_{wl}$.

Table 1. Characteristics of the Scots pine plantations*

	Plot			
	1	2	3	4
Leaf area index (projected) ($m^2\,m^{-2}$)	2.4	3.1	2.7	3.0
Trees				
Number (ha^{-1})	608.0	321.0	1725.0	1178.0
Mean DBH (cm)	23.3	14.6	17.0	20.3
Mean height (m)	15.0	15.0	14.3	14.6
Crown depth (% of tree height)	52.6	28.6	44.8	52.9
Basal area ($m^2\,ha^{-1}$)				
Total tree	26.6	57.7	41.2	39.0
Sapwood	21.0	39.7	28.9	28.0
Volume ($m^3\,ha^{-1}$)				
Sapwood	136.5	296.9	186.0	183.1
Cambium and phloem	2.4	1.3	1.1	1.4
Stem	168.0	365.0	250.0	245.0
Dry weight ($Mg\,ha^{-1}$)				
Needle	5.6	6.2	5.8	6.7
Branches	31.1	28.4	25.9	31.2
Roots	12.3	18.2	14.9	16.0

* All data from Whitehead (1978) except branch and root weights which are based on information from elsewhere (see text).

Leaf water potentials of canopy foliage were estimated as xylem pressure potentials measured with a miniature pressure chamber designed for individual needle pairs (Scholander *et al.*, 1965; Roberts & Fourt, 1977).

Cambium and phloem. On three trees on both Plots 1 and 2, dendrometer gauges with a resolution of 0.01 mm were attached immediately below the base of the live crown to record diurnal shrinkage throughout the year. All diurnal changes in diameter were attributed to the gain or loss of water from cambium and phloem since sapwood volume changes are negligible (Richards, 1973). The storage capacity of the cambium and phloem or the maximum amount of water which can be considered to be available was calculated from the maximum diurnal change in diameter of the stem.

Branch, root and stem sapwood. In a sample of sapwood of specific gravity ρ_f, the volume fraction of the wood occupied by water, ϕ, is given by Waring & Running (1978) as:

$$\phi = 1 - \frac{\rho_f}{\rho_s} \qquad (2)$$

where ρ_s is the density of solids (lignin and cellulose). The volume fraction of this water which can be considered to be available, ϕ_a, is:

$$\phi_a = \frac{R_{sw} - R_b}{100} \qquad (3)$$

where R_{sw} is the relative water content of the sapwood, and R_b is the fraction of bound water, i.e. water which is held tightly, such as water of hydration, and cannot be removed by physiological forces.

The volume of water considered to be available, V_a, is therefore given by:

$$V_a = V_{sw} \cdot \phi_a. \qquad (4)$$

V_{sw} is the volume of the sapwood and is obtained from

$$V_{sw} = \frac{W_{sw}}{\rho_d} \qquad (5)$$

where ρ_d is the specific gravity of dry sapwood, and W_{sw} is the weight of dry sapwood. The storage capacity of the sapwood is given by equation (4) when $R_{sw} = 100$.

Measurements of diurnal and seasonal changes in sapwood relative water content were made on cores from the outer 2 cm of sapwood at a height of 1.3 m. The cores were extracted with an increment borer before 0900 hours and trimmed in a 'Perspex' block to a constant volume of 0.312 cm³, sealed in air-tight glass vials, then weighed fresh, oven-dried at 80°C for 48 h and reweighed. Relative water content of the sapwood, R_{sw}, was calculated from

$$R_{sw} = \frac{W_{fs} - W_{ds}}{(V_f - V_s)\rho_w} \cdot 100 \qquad (6)$$

where W_{fs} and W_{ds} are the fresh and dry weights of sapwood; ρ_w is the density of water; V_f is the fresh volume of the sapwood sample; and V_s is the volume of the solids, cellulose and lignin.

The volume of solids was derived assuming a constant density, ρ_s, of 1530 kg m^{-3} (Skaar, 1972), from:

$$V_s = \frac{W_{ds}}{\rho_s} (\mathrm{m}^3). \qquad (7)$$

Seasonal changes in R_{sw} were determined from the mean values of five cores taken fortnightly from each plot.

The moisture characteristic of sapwood was measured by equilibrating sapwood segments (18 mm diameter × 4 mm) above a series of salt solutions in air-tight glass jars (500 cm³ in volume) in a water bath maintained at 25 ± 0.01 °C for 42 days (Jarvis & Jarvis, 1963). The samples were not more than 10 mm away from polyurethane foam saturated with the salt solution. At equilibrium, R_b was 20% of the total held in saturated tissue, leaving 80% available for extraction (Fig. 1). This is consistent with previous reports (Siau, 1971; Skaar, 1972).

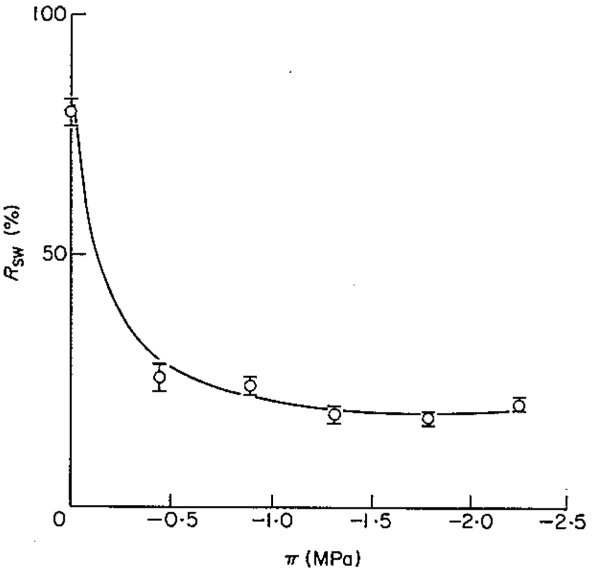

Figure 1. Relative water content (R_{sw}) of Scots pine sapwood equilibrated over NaCl solutions of a range of solute potentials (π). Each point is the mean ± 1 SE of five replicates. $R_{sw} = 100e^{0.468\pi + 20.20}$, $r^2 = 0.99$.

$100e^{4.679(\pi - 0.111)} + 20$

If the specific gravity of dry sapwood averages 420 kg m^{-3}, 1 Mg of wood has a volume of 2.38 m³, a maximum water content of 1.73 m³ and can hold 1.38 m³ of available water.

π is −MPa

Results

During 1977, predawn water potentials never fell below −0.4 MPa and the trees did not experience prolonged water stress. This indicates that soil water contents were always high enough for phloem and cambium to be recharged at night (Ritchie & Hinckley, 1975).

Table 2. The water storage capacities of different tissues in four Scots pine stands*

	Plot 1		Plot 2		Plot 3		Plot 4	
Tissue	(m^3 ha^{-1})	(%)	(m^3 ha^{-1})	(%)	(m^3 ha^{-1})	(%)	(m^3 ha^{-1})	(%)
Foliage	4.5	4	5.0	2	4.6	3	5.3	3
Cambium and phloem	1.0	0.8	0.5	0.2	0.4	0.3	0.6	0.4
Stem sapwood	71.7	58	156.0	74	97.7	67	96.2	63
Branch sapwood	33.6	27	30.7	14	28.0	19	33.7	22
Root sapwood	13.3	11	19.7	9	16.1	11	17.3	11
Total	124.1		211.9		146.8		153.1	

* 608, 3281, 1725, and 1178 trees per ha on Plots 1, 2, 3 and 4, respectively. Water storage capacity is the volume of the tissue × the possible change in relative water content and is equal to the maximum amount of 'available' water.

The total amount of 'available' water was largest on the plot with the highest population density, Plot 2, and least on the plot with the lowest population density, Plot 1 (Table 2). By far the largest part of the 'available' water was in the stem sapwood and the smallest part in the cambium and phloem: the foliage, cambium and phloem together contained less than 5% of the 'available' water. The proportion of 'available' water in the stem sapwood increased with increasing population density from 53% to 74% but there was more storage in the branch sapwood on Plot 1 than on Plot 2 because the weight and volume of the branches was slightly larger on Plot 1 (Table 4).

Relative water content of the needles always exceeded 80% and changed less than 10% on any day (Fig. 2). Lower values were only obtained when severed branches were allowed to dry out (Fig. 2).

Changes in phloem and cambium thickness typically followed changes in needle water potential (Fig. 3) as also found by Richards (1973) and Lassoie (1975). The largest diurnal change of the year was on 29 April 1977 (day 119) when the diameter of the trees decreased 3% in dry weather following a period of rain. Assuming that the cambium and phloem together were 3 mm thick, this represents a water loss of about 0.7 m^3 ha^{-1} day^{-1} (0.07 mm day^{-1}).

Figure 4 shows that at 06.00 hours R_{sw} was effectively constant with height in the outer sapwood. However, on bright sunny days, R_{sw} varied with height and time of day, indicating that water was initially withdrawn from the top of the stem (Fig. 5).

Generally, there was close agreement between values of R_{sw} at 1.3 m on all four plots, although the values were sometimes higher on the plot with the

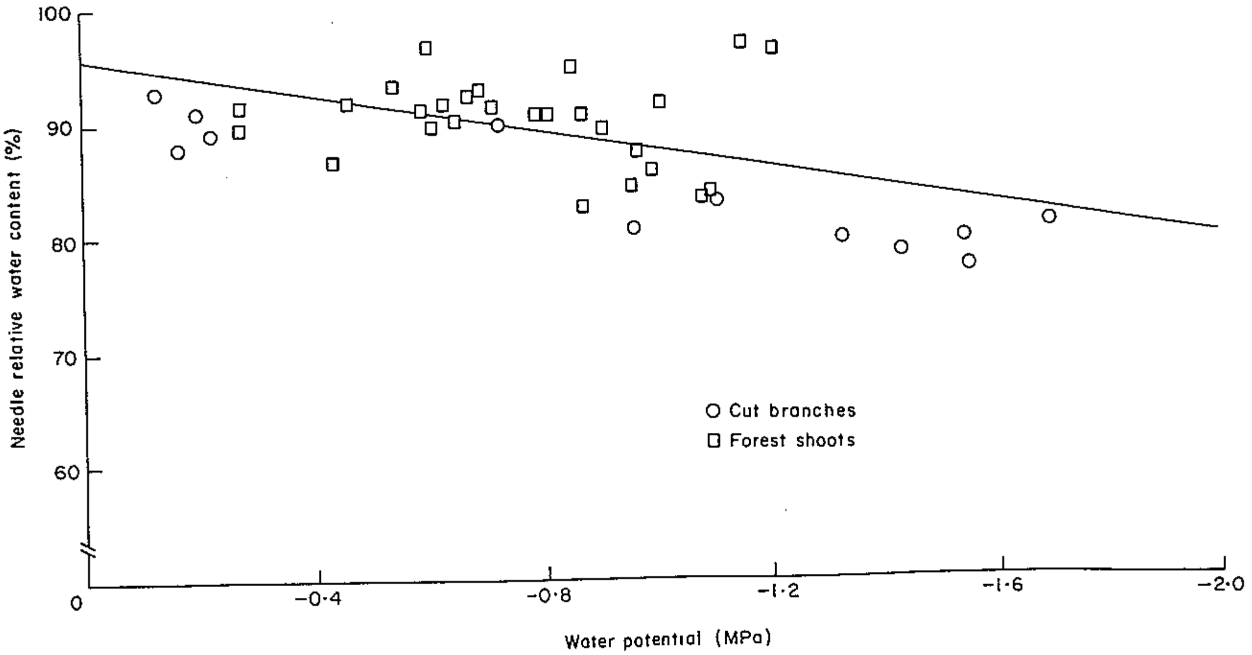

Figure 2. The relationship between needle relative water content (R_l) and water potential (ψ_l) measured with the pressure chamber during June and July 1977. $R_l = 95.2 - 7.7\psi_l$, $r^2 = 0.32$.

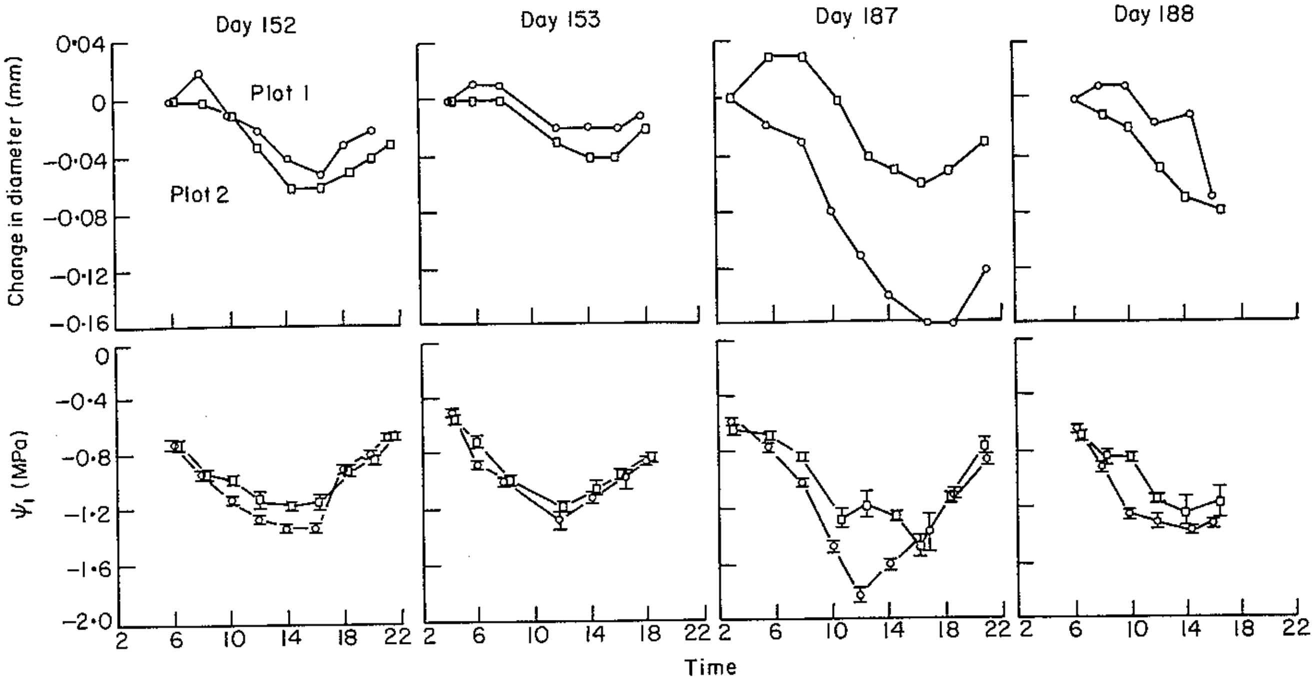

Figure 3. Diurnal changes in stem diameter at the base of the crown and needle water potential (ψ_l) (mean of five samples ± 1 SE). In June (days 152 and 153), water potential varied less than 0.8 MPa diurnally; in July (day 187), diurnal variation exceeded 1.2 MPa on Plot 1 and 0.8 MPa on Plot 2 with proportional changes recorded in diameter.

lowest population density, Plot 1, than on the plot with the highest density, Plot 2 (Table 3). The diurnal fluctuations in R_{sw} were larger on Plot 1 than on Plot 2 (Table 4). The largest changes in R_{sw} were decreases of 15% from 10 July (day 191) to 12 July 1 (day 193) on Plot 1 and of 12% from 9 July (day 190) to 10 July (day 192) on Plot 2. These decreases correspond to the extraction from the stem sapwood alone of 1.4 and 2.4 mm of water, respectively.

The largest changes in R_{sw} within any 2-week period were decreases between 31 December 1976 (day 364) and 14 January 1977 (day 14) (see Fig. 6a). This was a warmer period after freezing weather. The decreases of 28% and 26% on Plots 1 and 2, respectively, correspond to extraction from the sapwood of 25.1 and 50.7 m^3 ha^{-1} (2.5 and 5.1 mm). In contrast, the largest change in R_{sw} during the growing season was a mean increase of 12% from 17 June (day 168) to 5 July (day 186) 1977.

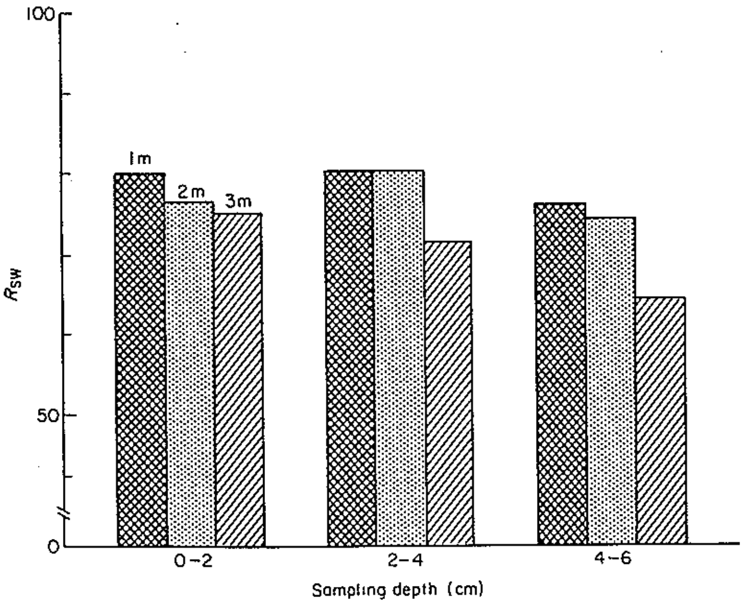

Figure 4. Relative water content (R_{sw}) at three heights above the ground and at different distances across the sapwood radius on a Plot 1 tree. Each core was subdivided into three sections after collection at 06.00 hours on 12 July 1977.

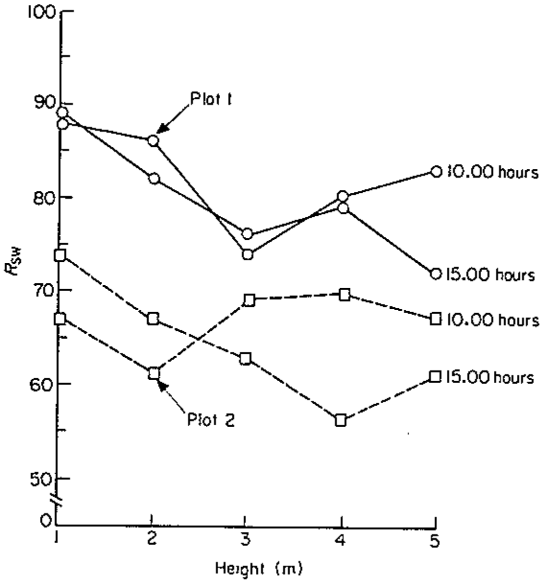

Figure 5. Relative water content (R_{sw}) of the outer 2 cm of sapwood at different heights and times on a sunny day, 7 July 1977.

On 14 January 1977 (day 14), the sapwood in all four plots was saturated (Fig. 6a). However, at least six times throughout 1977, R_{sw} was reduced to 30% below saturation in the outer 2 cm of sapwood at 1.3 m. If applicable to all sapwood, a 30% decrease in R_{sw} represents an extraction of 26.9 m^3 ha^{-1} (2.8 mm) and 58.5 m^3 ha^{-1} from all the sapwood of Plots 1 and 2, respectively.

Transpiration rates were highest during May and June, decreasing in the autumn and winter months (Fig. 6b). Over short periods, the trends in water deficit ($100-R_{sw}$) generally followed the trends in transpiration rate (Fig. 6a, b). On days when evaporation from wet foliage occurred for more than half the daylight hours there was no substantial reduction in sapwood water content. R_{sw} reached a minimum on 28 September 1977 (day 271) after a period of high transpiration rates, after which it increased slowly as transpiration rates fell during the autumn.

Table 3. Average values of R_{sw} measured at a height of 1.3 m in stems of Scots pine on Plots 1 and 2 on different sampling dates

	R_{sw}		
Julian Date	Plot 1		Plot 2
364 (1976)	72		72
14 (1977)	100		98
25	83	*	75
39	77		78
44	92	**	86
55	87		83
67	75		72
72	81		84
80	75		74
99	75		73
115	76	*	70
124	78		74
143	72	*	65
154	76		73
168	83		83
186	72		70
195	60	**	75
212	77		75
226	76	**	69
240	80	**	73
251	80		78
271	69		67
289	78	**	64
307	73		72
323	85	**	75
341	76		71
364	84	**	77

Differences between plots are significant at 5% (*) and 1% (**) level

Discussion

We have estimated that the maximum storage capa-

Table 4. Relative water content of sapwood, R_{sw}, measured at a height of 1.3 m in stems of Scots pine during July 1977

	Plot 1				Plot 2			
Julian Date	R_{sw}*	SE	ΔR_{sw}	V_a (mm)‡	R_{sw}*	SE	ΔR_{sw}	V_a (mm)‡
188	69	6	+13†	1.2	71	5	+8	1.6
189	82	1	−1	0.2	79	2	0	0
190	81	2	+4	0.4	79	4	−4 }†	0.8
191	85	3	−13†	1.2	75	2	−8 }†	1.6
192	72	4	−2	0.2	67	4	0	0
193	70	2	+2	0.2	67	3	+4	0.8
194	72	2	−12†	1.1	71	4	+4	0.8
195	60	3			75	1		

* All values of R_{sw} are means of five measurements taken before 09.00 hours

† Significant at $P=0.05$

‡ Estimated net change in stem sapwood for stand (1 mm = 10 m^3 of water per ha)

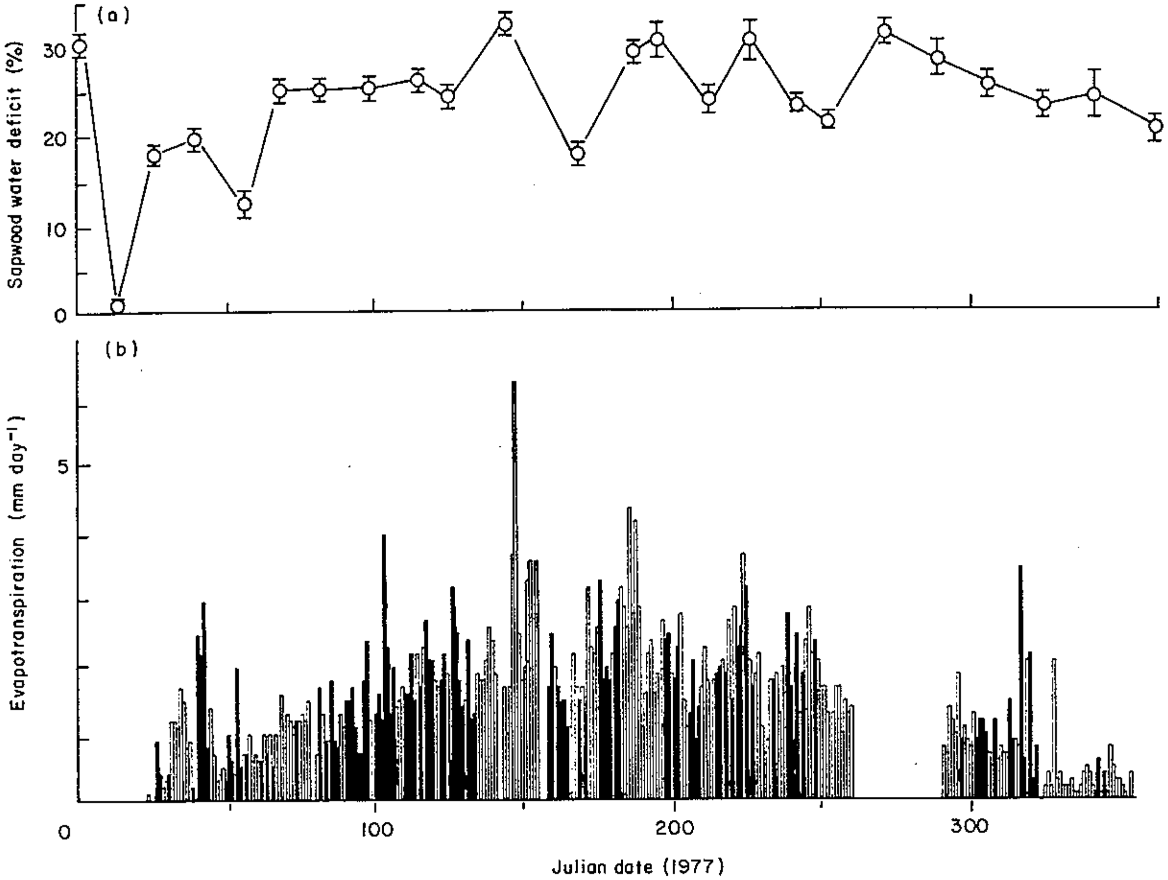

Figure 6. Relation between sapwood water deficit ($100-R_{sw}$) and estimated transpiration rate. (a) Sapwood water deficit through 1977 shown as mean of all twenty trees sampled on the four plots ± 1 SE. (b) Daily transpiration rates for the forest canopy (see text). The open columns indicate transpiration when the canopy was dry, and the closed columns indicate evaporation from a canopy at least partly wet for more than half the daylight hours. The automatic weather station failed between 18 September (day 261) and 16 October 1977 (day 289).

city, or the amount of 'available' water, in the 40 year-old Scots pine trees on Plot 2 exceeded 200 m^3 ha^{-1} (20 mm) and that over 95% of this water is stored in the sapwood. This figure of 20 mm is similar to the estimated storage capacity of 27 mm in the main stems of 450 year-old Douglas-fir in Oregon, U.S.A. (Waring & Running, 1978). Such storage capacities are closely related to the volume of the sapwood which depends upon the development of the canopy.

As a canopy closes, the sapwood basal area becomes constant since it is directly proportional to the area of foliage on the tree (Grier & Waring, 1974; Whitehead, 1978) which reaches a ceiling. Had the leaf area index been similar on all the plots, we would have expected similar sapwood basal areas and hence largely similar water storage capacities, irrespective of the numbers or size of trees on the plots. Although the water storage capacity of sapwood is larger in individual trees of large diameter than in small trees, there was more storage on Plot 2 than on Plot 1 because of the much larger numbers of stems present per hectare on Plot 2. However, the storage capacity on Plot 2 was less than twice that on Plot 1 although there were nearly four times as many trees present. Water storage capacity on a ground area basis, like transpiration rate (Whitehead, Jarvis & Waring, in preparation), is more closely related to the total sapwood basal area and hence the leaf area index than to any other stand characteristic.

Our definition of storage capacity as the maximum amount of water which can be considered to be available for transpiration is probably adequate for foliage, cambium and phloem, but may result in over-estimation of the storage capacity of the stem, branch and root sapwood. We have assumed that up to 80% of the water present is available since the moisture characteristic curve (Fig. 1) indicates that 80% of the water present in the sapwood can be easily removed.

Sapwood water deficit ($100-R_{sw}$) fluctuated throughout 1977, as shown in Fig. 6a, but never exceeded 30%. This is less than the seasonal changes of over 40% reported by Chalk & Bigg (1956) in *Picea sitchensis*, by Gibbs (1958) in many species including *Tsuga canadensis*, *Pinus strobus* and *Larix europea*, by Rothwell (1974) in *Pinus contorta* and by Waring & Running (1978) in Douglas-fir, and may be a consequence of differences in the climate and weather, leading to lower transpiration rates at Roseisle. In none of the studies cited was R_{sw} reduced by 80%. The maximum reduction found was 52% in Douglas-fir (Waring & Running, 1978).

The several months necessary for sapwood recharge during the winter is consistent with the findings of Waring & Running (1978) and suggests that cavitation and air entry into the tracheids has occurred and is not readily reversible. Substantial sapwood water deficits remained during freezing conditions in December, probably because of the low hydraulic conductivity of cold soil and frozen roots. This may also explain the decrease in R_{sw} during late January and February since air vapour pressure deficits did not exceed 0.5 kPa and evaporative demand was low.

The occasionally significant differences in R_{sw} between Plots 1 and 2 (Table 3) may be explained by the slightly higher wood density (ρ_d) in the trees on Plot 2 than on Plot 1 (average values of 468 ± 4 kg m^{-3} and 489 ± 4 kg m^{-3} at 1.3 m above the ground on Plots 1 and 2, respectively). In more dense wood, the volume fraction of water is less and would therefore be expected to vary from day to day with larger amplitude.

The results of this study are consistent with those of Waring & Running (1978) and hence are in marked contrast to those of Roberts (1976) on Scots pine at Thetford Forest in south east England. Robert's experiments were done in October 1975, after a dry summer when R_{sw} was rather low. In one experiment, the experimental tree had an initial R_{sw} of 38 to 41% from the base to the top and Roberts observed only a 1% decrease in R_{sw}. In another tree the initial values of R_{sw} were 48–62% and a 10% decrease occurred. We suggest that he observed only small changes in R_{sw} because the sapwood water reserves were already substantially depleted.

If water is equally available from all the stem sapwood, 10–15 m^3 ha^{-1} (1–1.5 mm) of water could be available each day for transpiration and possibly more for short periods during abruptly changing weather conditions (Table 4). Transpiration from this Scots pine forest rarely exceeded 3 mm day^{-1}, so that over short periods 30% to 50% of the transpired water could be derived from water stored in the stem sapwood. When the soil is very cold, it is possible that almost all the transpired water is from internal storage.

Sapwood water content and dry wood density both affect the hydraulic conductivity of tree stems (Puritch, 1971; Gregory, 1972; Waring & Running, 1978). Laboratory studies on small wood blocks by Puritch (1971) showed that a decrease in R_{sw} of 50% reduces the conductivity of sapwood by 94% relative to its value at saturation, and Gregory (1972) concluded that an increase in dry wood density from 300 to 500 kg m^{-3} decreases conductivity by almost 100%. Therefore the higher values of R_{sw} associated with lower values of ρ_d in the trees on Plot 1 than on Plot 2 probably result in the storage tissues being more easily refilled than in the trees on Plot 2. Thus there is a feed-back effect to maintain higher values of conductivity and relative water content in more rapidly grown, less dense wood.

In summary, we conclude that sapwood in conifers serves as a major reservoir from which up to 50% of the water transpired may be withdrawn over several days.

Acknowledgments

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