Journal of Experimental Botany, Vol. 30, No. 116, pp. 459–471, June 1979

Estimating Water Flux through Stems of Scots Pine with Tritiated Water and Phosphorus-32

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Received 4 December 1978

ABSTRACT

The radioisotopes of tritium (^{3}H) and phosphorus-32 (^{32}P) were simultaneously injected into the conducting tissue of more than 40 Scots pine trees over a 6 month period. Analysis of core samples indicated that ^{32}P and ^{3}H are transported by mass movement at similar rates. ^{3}H exhibits diffusion as well as mass flow properties. The strong beta emission of ^{32}P at the bark surface was monitored to determine the velocity of the pulse. Core samples provided an estimate of the volume of water-filled conducting tissue. The calculations of flux were compared with actual uptake by two trees severed at their bases and supported in water-filled containers. Over a 5 d period, periodic estimations of cumulative water uptake showed an excellent linear relationship with measured uptake ($r^2 \geqslant 0{\cdot}98$). Refinements in the model are discussed, emphasizing the importance of assessing diurnal variation in sapwood water content.

INTRODUCTION

Evaporation of water from forest canopies can be accurately estimated with the Penman–Monteith equation (Monteith, 1965) by characterizing the climate and certain physical and physiological properties of the foliage (Jarvis, James, and Landsberg, 1976).

However, this approach requires estimation of foliage area and stomatal conductance for each component of the forest canopy. Because it is laborious to obtain this information, the approach has rarely been applied. Alternatively, a tracer can be used to follow water flow through a sample of stems representing different species or size classes in a forest, and the total evaporation can be obtained by integration.

The most obvious choice is the radioisotope, tritiated water (^{3}H). However, tritium is a very weak beta emitter and can at present be measured only in the laboratory (Wang, Willis, and Loveland, 1975). Samples of the twigs or foliage must be collected and analysed to establish the mean residence time of the tracer within each tree to permit an integrated estimate of transpiration over a period of days or weeks (Jordan and Kline, 1977; Kline, Reed, Waring, and Stewart, 1976).

Where access to the crown is difficult or where more frequent estimates of water

flux are required, the strong beta emitter, ^{32}P has often been used. Unfortunately, no study has simultaneously compared the movement of ^{32}P and ^{3}H through trees. The movement of ^{32}P has been compared with estimates of water using the heat-pulse method (Klemm and Klemm, 1964; Heine and Farr, 1973), a technique that tends to underestimate actual sap velocities (Marshall, 1958; Doley and Grieve, 1966; Morikawa, 1972; Heine and Farr, 1973) and is not very accurate in large stems (Swanson, 1972; Lassoie, Scott, and Fritschen, 1977).

In this paper we describe a method developed for estimating water flux through stems of Scots pine and compare the transport properties of ^{32}P and ^{3}H. We also cut through the stems of two trees *in situ*, and supported them with their bases in water to calibrate ^{32}P estimates of water flux with the amount of water taken up by the trees.

MATERIAL AND METHODS

Site description

The experiments were done in a 40 year old Scots pine (*Pinus sylvestris* L.) spacing experiment established by the Forestry Commission on sand dunes along the Moray Firth in northern Scotland (58° N-lat., 4° W long.). The trees averaged 15 m in height, and stocking densities were 608 and 3281 trees ha^{-1}. The most open stand had a maximum projected leaf area index of 2·4, whereas the densest had a leaf area index of 3·1 (Whitehead, 1978). The leaf area index of Scots pine varies throughout the year with a maximum in June (Rutter, 1968).

Injection and monitoring of isotopes

Holes 10 mm in diameter were drilled downward at angles of about 5° into the conducting tissue of the trees at a height of 500 mm above the ground. Glass tubing, 100–150 mm long and filled with distilled water, was immediately inserted into each hole in such a way as to permit most trapped air bubbles to escape. Fine nylon tubing, 1 mm in diameter, was inserted inside the glass tubing, and any remaining air bubbles were sucked out. Once water uptake was clearly established, the isotopes were injected into the water with a bayonet-shielded hypodermic syringe. Within about an hour the contents of the glass tube disappear. The injection tube is then removed.

More than 40 trees—half in the open and half in the dense plantation—were injected during a 6 month period. As many as 10 per hour were labelled with a maximum of 2 mCi ^{32}P (as orthophosphate in dilute HCl, pH 2–3) and ^{3}H. Enough isotope was injected so that beta radiation could be monitored (10–100 cps) at the bark surface with a thin-window Geiger counter (Mini monitor type 5810). The amount of isotope required depended on the tree's diameter and the depth to which the conducting tissue was labelled. Usually the same trees could be injected each month because ^{32}P, which remains in the foliage and phloem, has a half-life of only 14·3 d and because ^{3}H is transpired from the trees.

The leading edge of the pulse, defined as a surface activity of 5 cps, was monitored with the Geiger counter as the isotope moved as much as 6 m above the injection site. Marking pins were used to plot the upward spiral movement of the isotopes.

Periodically, wood cores were extracted with a 'Pressler' increment borer from the region of the trees where the pulse had been located with the Geiger counter. The cores were immediately inserted into a Plexiglass block and this scanned with a portable scaler ratemeter (Nuclear Enterprises 5016 with Beta probe BP5). The block was designed so that the core could be advanced 10 mm at a time, counted, and trimmed. Then the segments were dropped into glass vials (5 ml) and capped for laboratory analyses.

In the laboratory, the vials with wood cores were weighed and then prepared for ^{3}H analysis (Jordan and Kline, 1977). After weighing, 2 ml distilled water were added to the vials which were then recapped and allowed to remain at room temperature for 24 h. With a syringe, 0·5 ml solution was extracted and added to a scintillation cocktail (toluene:Triton X-100, 2:1, by vol., with a 4 g l^{-1} 2·5-diphenyloxazole). A Beckman liquid scintillation counter (Model 200) was adjusted so only 1% of the ^{3}H and 4% of the ^{32}P registered in channels C and A. At a gain setting of 2·5, the counting efficiency for ^{3}H was about 35%.

The wood cores were drained and dried at 70 °C for 48 h. Wood density and moisture content were determined before cores were discarded as radioactive waste. All vials were cleaned thoroughly before re-use.

Water-filled volume of conducting tissue

The cross-sectional area of sapwood varies according to species, foliage area, and sampling height. Cores were taken from the trees in at least two directions at a height of 1·3 m for estimation of the cross-sectional area of sapwood.

The flow of water through the conducting system is restricted to the water-filled spaces. Furthermore, about 20% of the water held in water-saturated wood is bound up in the cell walls, thus the volume available for flow can be calculated if the original volume, dry weight, and moisture content of a core are known (Siau, 1971), and the volume of flux can be determined if the linear velocity of the tracer is known (Fig. 1).

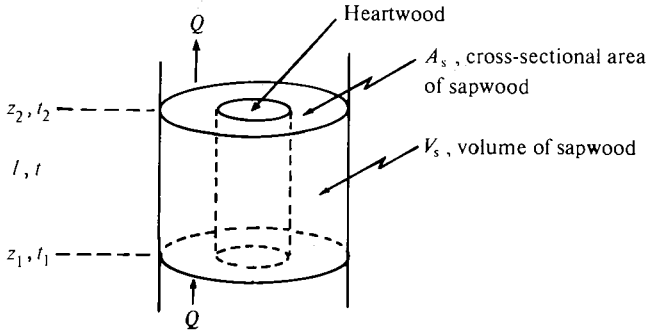

FIG. 1. Diagrammatic representations of location of measurements on water pathway in a tree stem.

A pulse of radioactivity moves from height z_1, at time t_1, to height z_2, at time t_2, a distance of h in time t. The linear velocity of the pulse is h/t. Assuming that the water flowing in the segment moves at the same velocity as the tracer, the volume flux of water in the segment, Q ($m^3 s^{-1}$) is

$$Q = \frac{h}{t} A_s (\phi - \phi_b) \tag{1}$$

where A_s is the cross-sectional area of sapwood, ϕ is the volume fraction of water, and ϕ_b is the volume fraction of non moving or 'bound' water (Fig. 2).

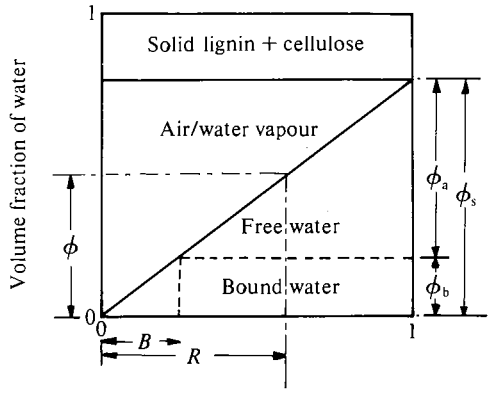

FIG. 2. Phase diagram illustrating the interrelationships between solid material, bound and available water, and air in wood (see Appendix for details of symbols).

In a sapwood of volume V_f, fresh weight W_f, and dry weight W_d

$$\phi = \frac{W_f - W_d}{V_f \cdot \rho_{H_2O}} = \frac{\rho_f - \rho_d}{\rho_{H_2O}} \tag{2}$$

where ρ_f ($= W_f/V_f$) is the density of wetwood, and ρ_d ($=W_d/V_f$) is the density of dry wood.

From the phase diagram,

$$\phi_b = B \cdot \phi_s \tag{3a}$$

or

$$\phi_b = \frac{B}{R} \cdot \phi \tag{3b}$$

where ϕ_s is the volume fraction of water in saturated wood, R is relative water content ($= \phi/\phi_s$), and B is that portion of the relative water content which is retained in cell walls and does not move under the prevailing pressure gradient. Substituting equations 2 and 3 into equation 1 gives

$$Q = \frac{h}{t} A_s \left[\frac{\rho_f - \rho_d}{\rho_{H_2O}} - B \cdot \phi_s \right] \tag{4a}$$

or

$$Q = \frac{h}{t} \cdot A_s \left[\frac{\rho_f - \rho_d}{\rho_{H_2O}} \right] \left[1 - \frac{B}{R} \right]. \tag{4b}$$

The volume fraction of water in saturated wood is

$$\phi_s = \frac{V_{H_2O}}{V_f} = \frac{V_f - V_{l,c}}{V_f} \tag{5}$$

where V_{H_2O} is the volume of water in the sample, and $V_{l,c}$ is the volume of solid material, largely lignin and cellulose.

$$V_{l,c} = \frac{W_d}{\rho_{l,c}} = V_f \frac{\rho_d}{\rho_{l,c}} \tag{6}$$

where $\rho_{l,c}$ is the density of the solid material ($\simeq 1{\cdot}53$, Siau, 1971). Substituting from equation 6 into equation 5:

$$\phi_s = 1 - \frac{\rho_d}{\rho_{l,c}}. \tag{7}$$

Substituting for ϕ_s in equation 4a from equation 7 or for R ($= \phi/\phi_s$) in equation 4b gives

$$Q = \frac{h}{t} A_s \left[\frac{\rho_f - \rho_d}{\rho_{H_2O}} - B\left(1 - \frac{\rho_d}{\rho_{l,c}}\right) \right]. \tag{8}$$

If a sapwood segment has constant water content and density between measurements and if isotope movement is uniform throughout, the average volume flux of water in the segment over the interval t can be calculated as

$$\bar{Q} = \frac{V_{sw}}{t} \bar{\phi}_a \tag{9}$$

where V_{sw} is the volume of sapwood in the segment and $\bar{\phi}_a$ is the average volume fraction of free water. This simplified calculation was used in the calibration experiment.

Calibration experiment

The calibration experiment involved supporting trees *in situ* with scaffolding while cutting through their trunks under water about 500 mm above ground level (Ladefoged, 1963; Roberts,

1977). The trees were situated next to metal towers that had been erected so that the crowns were accessible and stable. One tree, No. 1–50, with a diameter of 247 mm at 1·3 m, typified dominant trees in the open stand. Another, No. 2–51, with a diameter of 129 mm at 1·3 m, was a dominant tree in the dense stand.

During a 5 d period (28 April–2 May 1977), the water levels in the containers were checked at hourly or longer intervals, and the amount of water (± 100 ml) required to re-establish the original levels was recorded.

Cores of sapwood were sampled before and during the experiment to determine relative water content. Immediately after severing, 1 mCi ^{32}P and 1 mCi ^{3}H were injected about 40 mm deep into each tree 500 mm above the cut. Fifteen hours later at 0600 the next morning, we began monitoring isotope movement.

Resin did not appear to build up on the cut surfaces during the experiment. Afterwards, the trees were lowered to the ground and sections were cut at 1 m intervals up the stem. Total area and the area of sapwood stained with a dye based on diazotised toluidine (Shain, 1967) were measured on paper tracings made from the ends of each section. Knowing the area at each end assuming uniform taper, the volume of sapwood was calculated for each section.

RESULTS

Isotope experiments

Measurements of both ^{32}P and ^{3}H activities on nearly 200 core samples showed no evidence that ^{32}P lagged behind ^{3}H in its rate of ascent. The shape of the pulse as it moved upward varied somewhat, but generally the highest activity was in the outer 20 mm (Fig. 3). In any particular tree, the pulse maintained its shape as it moved upward (Fig. 4). Unless the entire radius of sapwood was labelled, activity remained restricted to the outer labelled zones above the injection site. Tritium

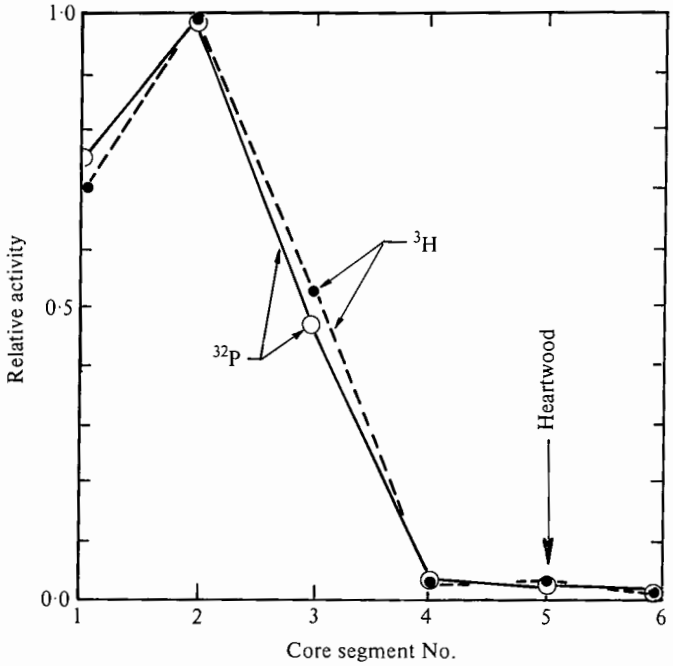

FIG. 3. Relative activity of 10 mm long core segments sampled at the leading edge of pulse, 1 m above injection site. Core segments numbered from the cambium inwards. Data from tree 2-52 collected at 1130 on 2 May 1977.

tended to spread more widely than ^{32}P and to remain at relatively higher concentrations after the front of the pulse has passed. However use of the Geiger-Müller scanner showed that all radioactivity left the point of injection.

We assumed that ^{32}P is carried along by mass flow and can adequately define the water transport pathways and rates through the stem for the width of the injection. Indeed ^{32}P may actually be a better indicator of water transport than ^{3}H because it diffuses more slowly. Furthermore, labelling only the outer 20–40 mm of the sap-

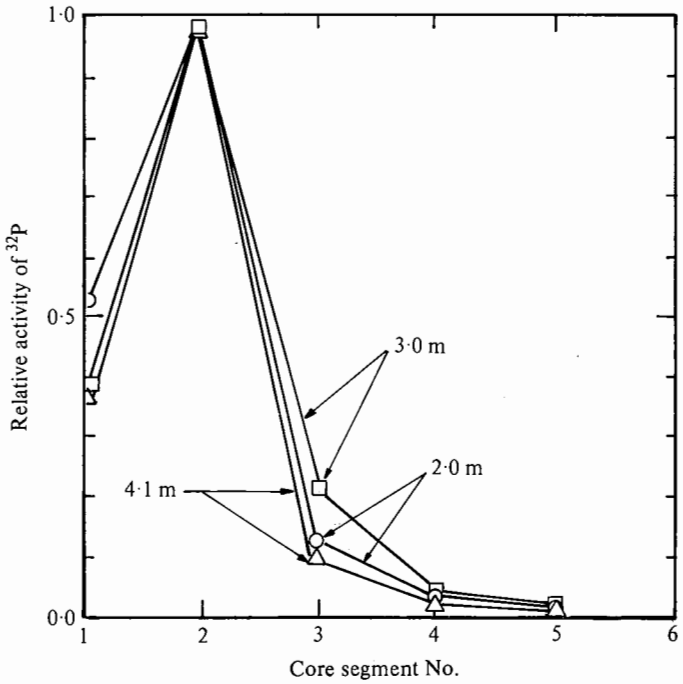

FIG. 4. Relative activity of ^{32}P presents a consistent pattern at the leading edge of the pulse. Measured in 10 mm long core samples collected 2–4 m above injection point of tree 1-50 from 29 April to 4 May 1977. Core segments numbered from the cambium inwards. The sapwood thickness varied from 64 mm at 2·0 m to 62 mm at 4·1 m height.

wood of conducting tissue may be adequate because the pattern of movement is consistent and all sapwood apparently participates to some extent. Thus, the volume flux may be estimated by externally monitoring the upward movement of ^{32}P and the physical characteristics of sapwood, e.g. volume, density, and relative water content.

Relative water content, R

Relative water content across the sapwood showed a slight but significant trend towards drier wood near the heartwood boundary during the summer (Fig. 5), as documented in other studies of conifers (Chalk and Bigg, 1956). We also observed some vertical differences (Fig. 5).

Over the course of a year, the relative water content in the outer 20 mm of sapwood varied from near saturation in January to 60% in August and September.

Variations of 5% in a single day were not uncommon, and daily variations larger than 10% occurred on 4 out of 9 consecutive days in June. The most striking change was an increase of between 20 and 25% in the calibration trees after their cut stems were immersed in water overnight.

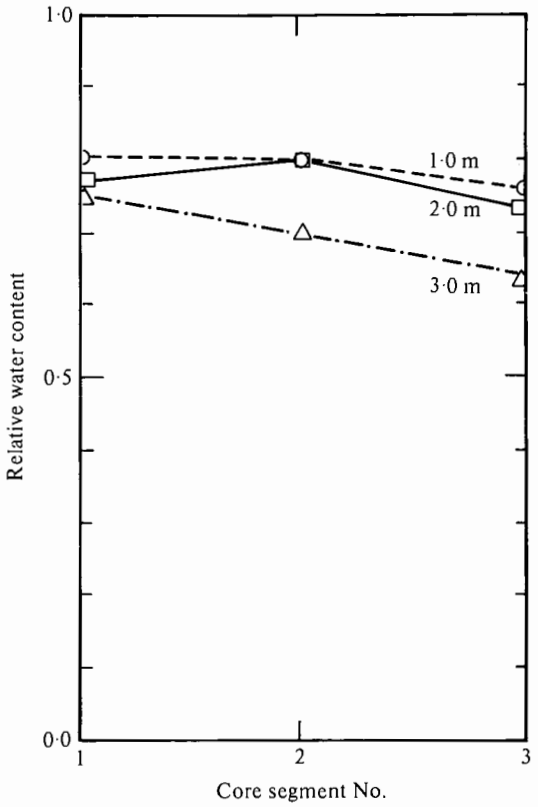

FIG. 5. Variation in relative water content R in 20 mm long core segments sampled 1, 2, and 3 m from injection point of tree 1-22 at 0600 on 12 July 1977. Core segments numbered from the cambium inwards.

Wood density, ρ_d

Density did not significantly change from the outer to inner sapwood, although some differences did occur among trees. A vertical decrease in density from 450 kg m^{-3} at 1 m to 350 kg m^{-3} at 10 m was common. At times, however, higher densities occurred at irregular intervals up the stem, probably from samples taken from old branch whorls (Table 1). Wood density varied sufficiently to cause major errors in the calculation of relative water content if an average density was assumed.

Calibration experiment

The calibration experiment was conducted during a period of cloudy and sometimes stormy weather from 28 April to 2 May 1977. The height of the leading edge of the pulse was recorded periodically as indicated in Table 2 (column 3). The cumulative volume (ΣV_{sw}) of sapwood above the point of injection was calculated

TABLE 1. *Examples of vertical variation in wood density (kg m^{-3}) from 20 mm deep core samples*

Values are means of 2–3 samples

Tree No.	Height (m)								
	0	1	2	3	4	5	6	7	8
2-52	440	370	390	390	380	380	370	360	340
1-52	450	450	420	400	390	380	370	—	—
2-51	420	420	400	400	390	390	—	—	—
2-28	—	480	450	410	410	410	400	—	—
1-21	—	430	410	390	340	380	—	—	—
2-25	—	540	520	500	520	440	—	—	—

from the vertical profile of cross-sectional area (column 4). The volume of wood through which the isotope had passed during an interval was the change in ΣV_{sw} during the interval ($\Delta\Sigma V_{sw}$) (column 5).

For a wood density of 430 kg m^{-3}, ϕ_s is 720 kg m^{-3} (equation 7). If R (column 7) was a constant 0·91 and if $B = 0{\cdot}2$, $\bar{\phi}_a = 0{\cdot}52$ (column 8). Column 9 gives $V_{sw}\bar{\phi}_a$. The cumulative predicted uptake, $\Sigma V_{sw}\bar{\phi}_a = \Sigma\hat{Q}$, is given in column 10. This is compared with the measured water uptake (ΣQ_m) in column 11 and Figs 5 and 6.

If major changes in R occurred between measurements at any point in the tree, the net gain or loss from the sapwood would have to be accounted for to accurately predict the flux. In the calibration trees, relative water contents throughout the first 3 m above the base averaged 0·91 ± 0·05 s.e. over the 5 d period. Some measure-

TABLE 2. *Calculation of cumulative water uptake ($m^3 \times 10^{-3}$) for tree No. 2-51 and comparison with measured uptake*

Date	Time	Pulse height	ΣV_{sw} ($m^3 \times 10^{-3}$)	$\Delta\Sigma V_{sw}$	ρ_d (kg m^{-3})	R	ϕ_a	$V_{sw}\phi_a$	$\Sigma V_{sw}\phi_a = \Sigma\hat{Q}$ ($m^3 \times 10^{-3}$)	ΣQ_m
28 April	0600	0·27	2·6	—	430	0·91	0·52	—	—	—
	1200	0·37	3·6	1·0	430	0·91	0·52	0·52	0·52	0·50
	1700	0·54	4·6	1·0	430	0·91	0·52	0·52	1·04	2·30
29 April	0700	0·74	7·0	2·4	430	0·91	0·52	1·25	2·29	3·95
	2000	1·12	10·1	3·1	430	0·91	0·52	1·61	3·90	4·45
30 April	0700	1·17	10·5	0·4	430	0·91	0·52	1·21	4·11	4·75
	1430	1·49	13·0	2·5	430	0·91	0·51	1·29	5·40	6·40
1 May	1200	1·61	13·8	0·8	420	0·91	0·51	0·41	5·81	7·53
	1500	1·79	15·2	1·4	420	0·91	0·51	0·72	6·53	7·80
	1700	1·91	16·1	0·9	420	0·91	0·51	0·46	6·99	8·56
2 May	0600	2·02	16·7	0·6	420	0·91	0·51	0·31	7·30	9·36
	1200	2·25	18·4	1·7	420	0·91	0·51	0·88	8·18	9·70
	1400	2·38	19·3	0·9	410	0·91	0·51	0·46	8·64	—

ments taken near dawn often reached 0·95: the significance of this variation will be discussed later.

DISCUSSION

The results generally support the contention that ^{32}P can serve as an adequate tracer of the major pathways for water transport (Owston, Smith, and Halverson, 1972). The Geiger-Müller tube scans show that the pulse remains coherent axially and analysis of radioactivity of cores shows little radial transport. The coherent nature of the pulse suggests that injection at different depths might permit, through destructive stem analysis, a precise assessment of the route water takes to different branches.

The injection procedure minimizes embolism at the time the isotopes are introduced. This results in low residual activity at the injection point and permits a lower dose to be used. If only the outer 20–30 mm of sapwood are injected, a 1 mCi dose is sufficient for almost any size of tree because the ^{32}P pulse remains in the outer sapwood. With the procedures outlined, isotopes no longer have to be introduced through the roots to prevent embolism (Owston *et al.*, 1972).

Core samples can adequately show the distribution of the isotopes. However, the narrow pulse and frequent spiral direction of the pathway suggest that autoradiographs of sectioned trees would give a more precise analysis (Smith, 1972). Because of the spiral ascent, one must sometimes bore holes at different angles to evaluate the distribution of activity across a wide band of labelled sapwood.

The decreasing relative water content observed toward the heartwood boundary could partly account for the slower ascent of isotopes in those zones (Swanson, 1974). As Puritch (1971) demonstrated from measurements of wood conductivity in *Abies grandis*, a small decrease in relative water content causes a large decrease in the transport of water. Of course, the older, inner sapwood possibly supplies water mainly to the older lower branches which generally have less foliage and are less well irradiated than limbs higher in the crown. Variations and changes in relative water content could account for some of the apparent inconsistencies in transport and uptake patterns interpreted from heat-pulse measurements (Swanson, 1972; Lassoie *et al.*, 1977; Doley and Grieve, 1966).

Although counts of isotope activity or autoradiographs indicate the pathways of water transport, accurate estimation of the flux requires knowing the relative water content. Seasonal and even diurnal variations in R are important in three ways. First, they reflect changes in storage that must be considered in estimating net flux through the stem. Secondly, any decrease in R exponentially reduces wood conductivity (Puritch, 1971), and thirdly, velocity measurements can vary by a factor of two, yet reflect the same flux if the volume of free water varies correspondingly.

The predicted fluxes consistently underestimated the measured fluxes by 7–8% (Figs 6 and 7). The kinds of errors that might account for this are pertinent to consider. From equation 8, underestimation of ρ_f, h, and A_s, or overestimation of ρ_d or B, apparently will result in an underestimation of Q.

Because the estimates of ρ_d were averaged for the stem sections through which

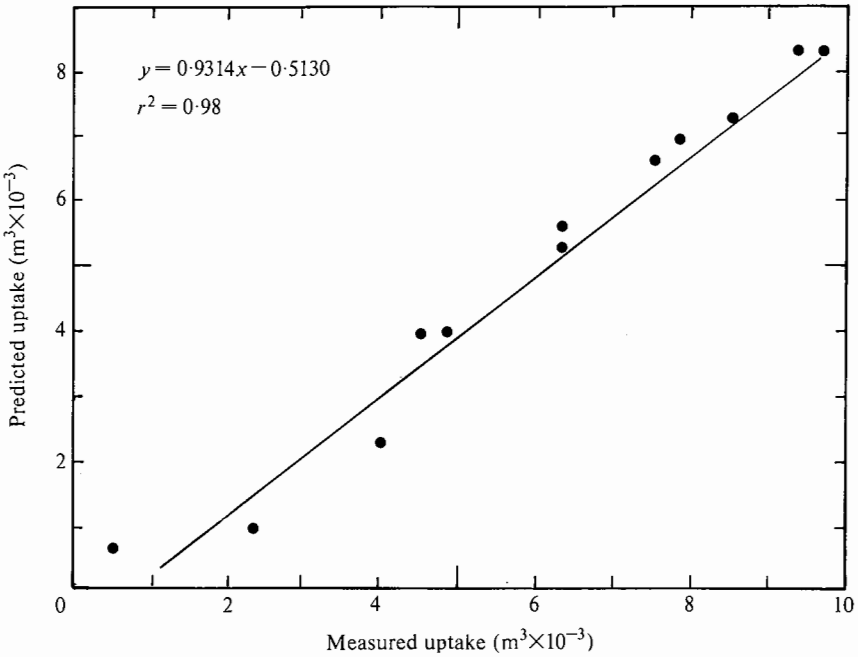

FIG. 6. Cumulative measured water uptake versus uptake predicted from isotope and core analysis for tree 1-50 from 28 April through 2 May 1977.

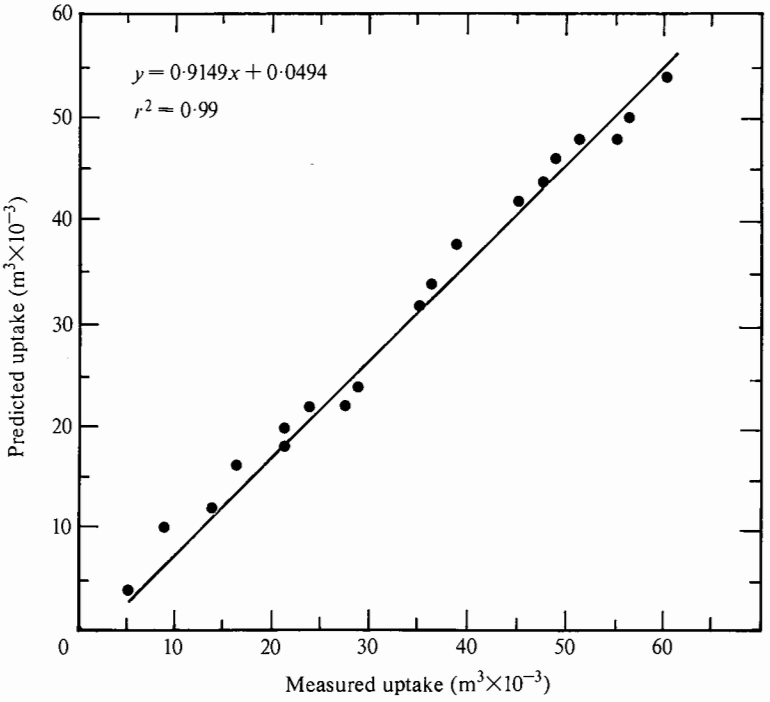

FIG. 7. Cumulative measured water uptake versus uptake predicted from isotope and core analysis for tree 2-51 from 28 April through 2 May 1977.

the pulse was moving, estimates of ϕ_a are inaccurate when the pulse extends to a height of many meters. A 10% error in ρ_d could lead to a 5% error in the estimates of Q. A_s also may be inaccurate, particularly when derived from sample cores alone. However, in the calibration experiment, we sectioned the trees and made tracings of the sapwood area on the cut surfaces. Thus, appreciable error in A_s is unlikely.

Our simplified model of water calculations assumed that all of the sapwood conducts at an identical rate. However, our data and the results of other studies, (e.g. Swanson, 1974) indicate that a parabolic pulse, with the most rapid water movement 2–3 cm in from the cambium, is more likely.

As long as the shape of the pulse remains consistent as it appears to do in a given experiment (Fig. 4), calculations of h assuming a square wave should not err greatly. However, the choice of 5 cps as an indicator of the leading edge of the pulse may mean that a significant difference in effective 'h' may result but this will not be a cumulative error. However a lower threshold of counting could not be resolved. The use of the 5 cps level gave a correspondence to as close as 7% to water uptake measured in cut trees. Some likely causes of this discrepancy are discussed below. It would be worthwhile in future to examine reasons why a single point injection becomes a pulse. For instance there is sufficient variation in wood properties, e.g. tracheid radii, lengths, numbers of pits per tracheid end wall, and tortuosities of pathways to cause spreading of the pulse. Clearly, however, in the present case the majority of the water transported is adequately monitored by use of the leading edge of the pulse. A consistent error in B could account for the deviation, and a value as low as 0·17 may be possible according to results obtained above equilibrated salt solutions. So an increased volume of 3% might be possible.

The cyclic pattern around the regression lines in Figs 6 and 7 may represent diurnal or nocturnal variation of R or ρ_f. We consistently measured some nocturnal uptake of water, particularly on the first night when R increased by 20–25%. An overall change of 5% in R, from an average of 91–96%, would result in an increase in the estimated water flux by 10%. That is more than enough to account for the entire deviation from the 1 : 1 correspondence with measured uptake. On balance, we feel that the assumption of constant R or ρ_f is probably the main reason for the underestimation of Q.

^{32}P can serve as a tracer of water transport and an estimator of flux through stems. The inexpensive technique permits up to ten trees an hour to be labelled and monitored over a period of days. When calculating flux from a stand, the procedure has the advantage of needing only an estimate of sapwood area at 1·3 m or at ground level; leaf area and climatic variables are not required. Future studies should recognize that the conducting tissue is a significant storage organ, as well as a pathway for water transport. Variation in relative water content should be taken into account to accurately calculate the flux of water and to interpret changes in stem conductance.

These experiments using ^{32}P and ^{3}H and others using ^{3}H (e.g. Kline *et al.*, 1976, and Kline, Martin, Jordan, and Koranda, 1970) have been carried out on various conifers and tropical hardwoods. From the experiments so far conducted, there

seems good reason to suppose that the technique will be successful in a wide range of woody species.

ACKNOWLEDGEMENTS

We thank the Conservator N.E. for permission to use the site and gratefully acknowledge the assistance and provision of facilities by other Forestry Commission staff from Newton Nursery. We also thank Professor P. G. Jarvis, Dr. D. D. Whitehead, and Mr. J. Landless (Department of Forestry and Natural Resources, University of Edinburgh) for practical assistance with these experiments, and Dr. A. J. Hayes and Mr. J. Allen for help in using the isotopes. This research was partly supported from a National Science Foundation Grant DEB 76-10765. This is paper 1222 of the Forest Research Laboratory, School of Forestry, Oregon State University, Oregon, U.S.A.

APPENDIX

Explanation of symbols used in text

A_s cross sectional area of sapwood
B bound water content
F free water content
M gravimetric water content $\left(\frac{W_f - W_d}{W_d}\right)$
(N.B. the volumetric water content $\frac{V_w}{V_f} = \phi$)
Q volume flux
$\hat{Q}$ predicted volume flux
R relative water content
V_f fresh volume of sample
V_{H_2O} volume of water in sample
V_{sw} volume of sapwood
W_d dry weight of sample
W_f fresh weight of sample
W_s saturated weight of sample
h distance moved by radioactive tracer
ρ_d density of dry wood (dry weight/fresh volume)
ρ_f density of fresh wood (fresh weight/fresh volume)
ρ_{H_2O} density of water
$\rho_{l,c}$ density of solid material in wood (lignin and cellulose) ($\simeq 1{\cdot}53$)
ϕ volume fraction of water
ϕ_a volume fraction of freely moving (available) water
ϕ_b volume fraction of water retained in walls and not moving (bound water)
ϕ_s volume fraction of water in saturated tissue

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