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FIELD MEASUREMENT OF TRANSPIRATION IN DOUGLAS-FIR

BY J. R. KLINE,* K. L. REED,† R. H. WARING‡ AND M. L. STEWART§

* *U.S. Atomic Energy Comm. Directorate of Licensing, Washington D.C. 20545, U.S.A. (formerly Argonne National Laboratory, Argonne, Illinois 60439, U.S.A.),* † *University of Washington, Seattle, Washington, U.S.A.,* ‡ *Oregon State University, Corvallis, Oregon U.S.A. and* § *formerly Argonne National Laboratory (now deceased)*

INTRODUCTION

This paper describes the measurement of transpiration rates in Douglas-fir (*Pseudotsuga menziesii*) (Mirb.) Franco in the field at the US/IBP Coniferous Biome research site at the Cedar River Watershed near Seattle, Washington and at the Andrews Experimental Forest near Eugene, Oregon. Tritiated water (HTO) was used as a tracer for water (Kline *et al.* 1970; Kline, Jordan & Rose 1971; Kline *et al.* 1972b; Kline, Stewart & Jordan 1972a). The tracer method is based on the theory of tracer dynamics which has been used for the measurement of the *in vivo* kinetics of biological systems (Bergner 1961, 1964a, b, 1965, 1966; Zierler 1964; Orr & Gilespie 1968; Ljunggren 1967; Shipley & Clark 1971; Sheppard 1962), as well as for the measurement of flow rates in such diverse systems as rivers, industrial processes and blood in organisms

The objectives of this study were: (1) to measure the rate of water transport in Douglas-fir in the field and (2) to extend the range of tracer measurements beyond previous limits and so to verify the generality of previous results.

MATERIALS AND METHODS

Nine trees at the Cedar River site and one large old tree at the Andrews site were injected with HTO (Table 1).

A known volume of HTO was injected with a calibrated hypodermic syringe into holes bored into the base of the trees. The holes were bored immediately prior to injection with a twist drill (3·18 mm diameter) or small increment borer, and were equally spaced around the base of the trees. The number of holes used for injection ranged from four on the smallest trees to twenty on the largest. All injections went directly into the sapwood of the trees, but did not extend into heartwood. The holes were sealed immediately after injection to prevent the escape of HTO.

The HTO solutions were calibrated for radioactivity, by comparison with standard solutions, using a liquid scintillation counter. Corrections for quenching and background were made for all samples. The unit of radioactivity used for the standards and all experimental samples was DPM cm^{-3} (disintegrations per min per cm^3). Corrections for radioactive decay were not made on samples collected during the experiment because of the long half-life of tritium.

The trees were sampled once or more daily after injection until HTO had passed completely through the tree. Samples were usually obtained by shooting twigs from the trees with a shotgun, but climbers collected some samples from the old-growth tree at the Andrews site.

Table 1. *Description of trees and amounts of tritiated water injected into trees in the Cedar River Watershed (CR) and the Andrews experimental forest (An)*

Tree	Height (m)	Inside bark (dbh*) (cm)	Sapwood thickness (cm)	Sapwood cross-section (cm²)	Number of injection holes†	Total HTO injection† (DPM) (×10⁹)	Date of injection
2 CR	18·7	23·0	3·94	236	8	8·82	11 Sept. 1972
3 CR	15·2	15·2	2·39	96·0	8	8·82	11 Sept. 1972
4 CR	18·0	27·9	3·70	280	9	9·92	11 Sept. 1972
5 CR	11·0	9·6	2·47	55·3	4	4·41	11 Sept. 1972
6 CR	18·3	16·7	3·10	132	8	8·82	11 Sept. 1972
7 CR	17·0	30·8	4·20	390	8	8·82	11 Sept. 1972
8 CR	14·6	12·0	2·26	68·9	4	3·86	11 Sept. 1972
9 CR	27·1	33·2	4·26	387	8	8·82	11 Sept. 1972
10 CR	24·8	47·9	7·53	954	8	8·82	11 Sept. 1972
1 An	75·6	134	10·4	4020	20	99·20	18 June 1972

* dbh, diameter at breast height.

† Each injection consisted of 1 cm³ of HTO per hole having a specific activity of 1·10 × 10⁹ DPM cm^{-3} at Cedar River and 4·66 × 10⁹ DPM cm^{-3} at the Andrews site.

At each sampling time, twigs and needles were collected from several parts of the canopy. Twigs and needles were separated and the samples combined for analysis. The samples were placed in plastic bags and frozen as soon as possible to prevent the loss of tritium. Water was extracted from the twigs by freeze-drying and the tritium counted by liquid scintillation methods (Stewart, Kline & Jordan 1971). The tritium activity, expressed

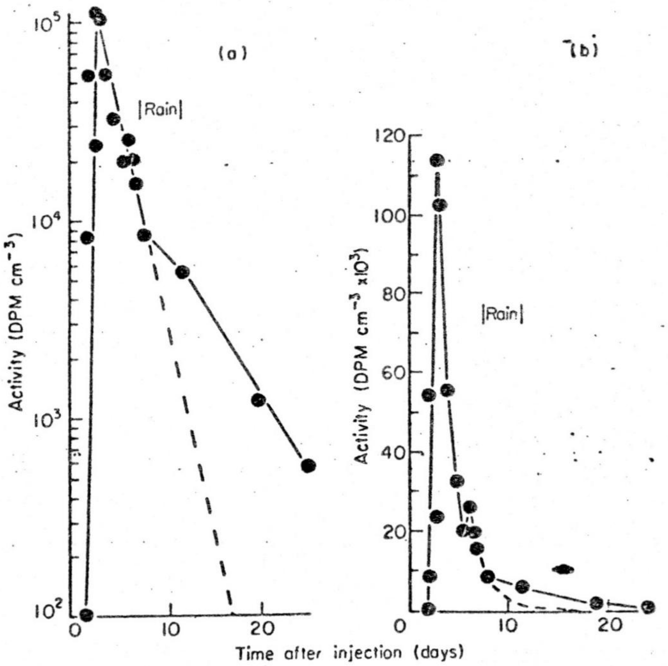

FIG. 1. Plot of HTO activity against time for tree number 6 on the Cedar River Watershed: (a) semilogarithmic, (b) rectangular co-ordinates. Steady rainfall occurred during the interval shown. The dashed lines show the extrapolations which were made to obtain expected transpiration rates if there had been no rain (see text).

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as DPM cm^{-3}, was plotted against time for each tree (Fig. 1) and the area beneath this curve measured to obtain transpiration rates for the trees. No mathematical function reliably describes the shape of the curves, so the area was measured by weighing the area of paper cut out, or by using a planimeter.

Measurements of solar radiation, air temperature and dew point temperature were used to make additional computations of transpiration rate at the Andrews site.

RESULTS AND DISCUSSION

Transpiration

The average transpiration rate ($\bar{F}$) of each tree (Table 2) was calculated using the Stewart-Hamilton equation (Zierler 1964):

$$M=\bar{F} \int_0^\infty f(t)dt \tag{1}$$

(Definitions of all mathematical symbols are given in Appendix A.) The value of the integral was calculated as the total area beneath the activity-time curve.

Estimates of transpiration rate are given for total periods and the period without rain for most of the Cedar River trees (Table 2). The estimate of transpiration rates of the whole period was obtained by integrating the total area under the curve during the full period of the experiment, including the rainy period (Fig. 1). The estimates of transpiration during the period without rain were obtained by extrapolating the curves on semi-logarithmic co-ordinates with the same slope that was established prior to the rainfall (Fig. 1) and integrating the resulting activity-time curve.

Daily average transpiration

The calculated transpiration rates (Table 2) are average daily rates for the full term of the experiments. The Stewart-Hamilton equation does not permit resolution into daily averages, since the assumption is made that the flow is constant during the measurement period (Zierler 1964). However, Orr & Gilespie (1968) have pointed out that the equation is not very sensitive to deviations in flow rate and can therefore be used successfully in systems where the assumption of constancy is not strictly true (Kline *et al.* 1971).

When weather data are available, it is possible to resolve the long-term average flow rates into daily averages using Montieth's development of the Penman equation for transpiration (Rutter 1968):

$$T_i = \frac{SR_n + \rho c\,(e_s - e)/r_a}{\lambda S + \lambda \gamma\,[(r_a + r_s)/r_a]} \tag{2}$$

The average transpiration rate for the entire period is given by:

$$\bar{T} = \frac{\bar{S}\bar{R}_n + \rho c\,(\bar{e}_s - \bar{e})/\bar{r}_a}{\lambda \bar{S} + \lambda \gamma\,[(\bar{r}_a + \bar{r}_s)/\bar{r}_a]} \tag{3}$$

assuming that

$$F_i/T_i = \bar{F}/\bar{T} \tag{4}$$

Substituting equations (2) and (3) into (4), we obtain the following expression for mean daily transpiration rate:

$$F_i = \bar{F}\left[\frac{S\,R_n + \rho c\,[(e_s - e)/r_a]}{\bar{S}\,\bar{R}_n + \rho c\,[(\bar{e}_s - \bar{e})/\bar{r}_a]}\right]\left[\frac{\bar{S} + \lambda/\bar{r}_a\,(\bar{r}_a + \bar{r}_s)}{S + \lambda/r_a\,(r_a + r_s)}\right] \tag{5}$$

Table 2. *Transpiration rates measured in Douglas-fir on the Cedar River Watershed and the Andrews experimental forest*

	Period without rain*				Total period		
Tree	Amount of HTO (DPM) (× 10^9)	Curve integral (DPM h cm^{-3}) (× 10^6)	Flow rate (l day^{-1})	Dates 1972)	Curve integral (DPM h cm^{-3}) (× 10^6)	Flow rate (l day^{-1})	Dates† (1972)
2 CR	8·82	5·11	41·4	11–19 Sept.	6·63	31·9	11 Sept.–6 Oct.
3 CR	8·82	1·21	17·5	11–19 Sept.	17·70	12·0	11 Sept.–6 Oct.
4 CR	9·92	5·51	43·2	11–19 Sept.	7·99	29·8	11 Sept.–6 Oct.
5 CR	4·41	10·10	10·4	11–19 Sept.	1·27	8·4	11 Sept.–6 Oct.
6 CR	8·82	5·86	36·0	11–19 Sept.	7·22	29·3	11 Sept.–6 Oct.
7 CR	8·82	—	—	NA	7·62	27·8	11 Sept.–6 Oct.
8 CR	3·86	7·14	13·0	11–19 Sept.	8·04	11·5	11 Sept.–6 Oct.
9 CR	8·82	—	—	NA	3·68	57·5	11 Sept.–6 Oct.
10 CR	8·82	1500	141	11–19 Sept.	2·24	94·5	11 Sept.–6 Oct.
1 An	99·20	4·48	530	18 June–21 July	NA	NA	NA

* Values in this section are average rates (trees 2–10) for the periods indicated when negligible rain fell.

† Dates show interval required for complete loss of HTO pulse. Values are averages (trees 2–10) for all weather conditions in the indicated time interval.

NA, not applicable.

If soil moisture stress, windspeed and temperature are not very variable during the period of the experiment, it may be assumed that $r_s \simeq \bar{r}_s$, $r_a \simeq \bar{r}_a$ and $\bar{S} \simeq S$, respectively. The daily transpiration rate is then principally a function of net radiation and saturation deficit both of which are easily measured and often available.

Average rates of transpiration for a 24-h day were calculated from equation (5) for the Oregon tree over a period of thirty-four days during which the overall mean transpiration rate was 22·1 l/h (Fig. 2). Constant stomatal resistance was assumed.

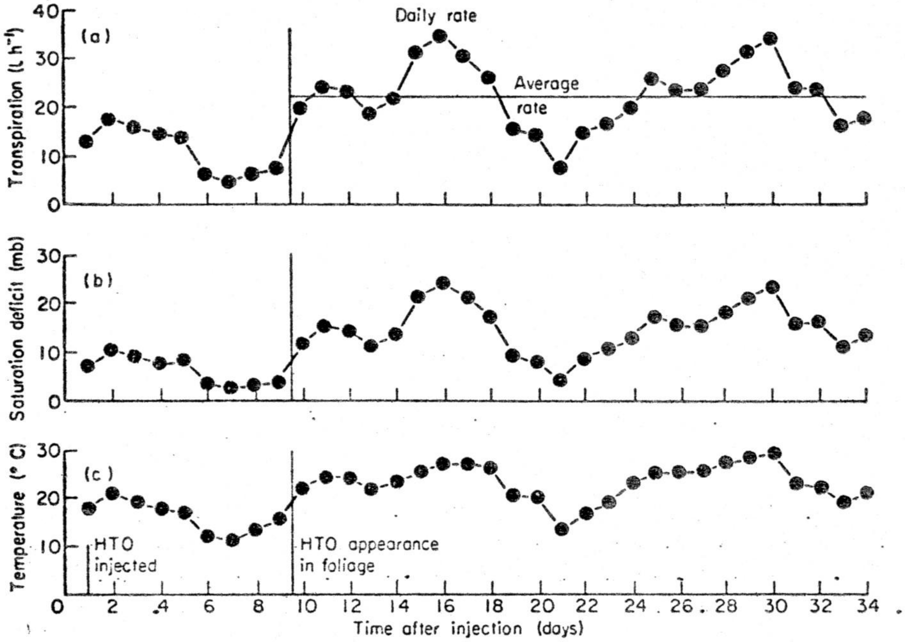

FIG. 2. Daily average values of transpiration in the Oregon tree (a), saturation deficit (b) and air temperature (c).

The main limitation to this method of allocation of transpired water to individual days lies in the assumptions that r_s and r_a are constant during the experimental period. Errors in the computed result occur if these assumptions are not met. The actual values of r_s and r_a, however, are not important.

Sap flow velocity

The flux (F) of liquid water through a flow system is equal to the product of the velocity of flow (Q) and the cross-sectional area (A):

$$F = Q\,A. \tag{6}$$

The conducting cross-sectional area of a tree is the cross-sectional area of sapwood, since the heartwood does not conduct. Thus:

$$A = \pi\,(R_t^2 - R_H^2) \tag{7}$$

Substituting equation (7) into equation (6) gives

$$F = Q\pi\,(R_t^2 - R_H^2) \tag{8}$$

A graph of F against $\pi(r_t^2 - R_H^2)$ would therefore be expected to yield a straight line

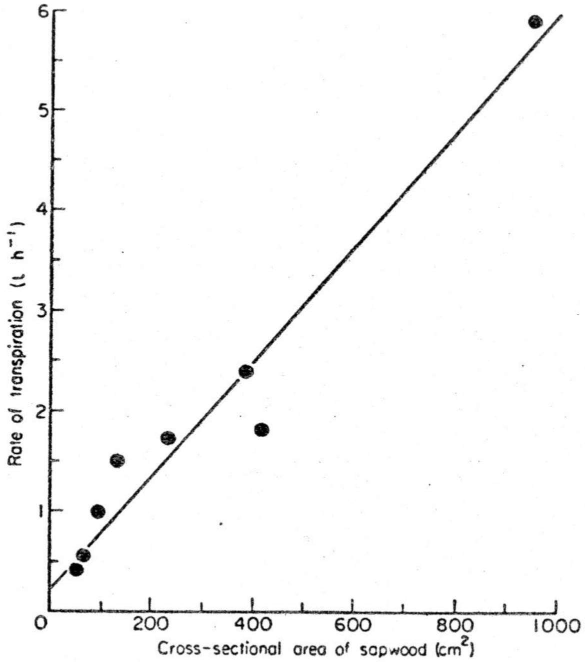

FIG. 3. The relationship between sapwood cross-sectional area and transpiration rate in trees from the Cedar River experiment. $F = 0{\cdot}21 + 0{\cdot}0057\,A$, $r^2 = 0{\cdot}95$.

with intercept of zero and slope Q (Fig. 3). The value of Q for the single large tree from Oregon (5·6 cm h^{-1}), which was measured at a different time and place, was similar to that for the Seattle trees (5·7 cm h^{-1}). This suggests that average sapflow velocities are consistent among individuals of Douglas-fir over a wide range of sizes and locations, though these measurements, made under conditions of low soil moisture stress, may be maximum values for the species.

The sapflow velocities, measured by the tritium method, agree well with the values for Douglas-fir saplings obtained by Hinckley & Scott (1971) and by Hinckley (1971) using a thermoelectric sap velocity meter. Hinckley & Scott's values range from 4·2 to 6·2 cm/h when averaged over several days. Differences among trees in their experiments were apparently due to different xylem sap pressures. This agreement suggests that measurements of sapflow velocity might be used to solve equation (8) for transpiration rates in Douglas-fir over the full range of sizes for the species. Hinckley's data, however, do show that considerable sapflow persists during periods when transpiration approached zero, perhaps because of recharge of the sapwood. This suggests that errors will result if too great a time resolution of transpiration is attempted using the thermoelectric method.

It would seem that reasonable estimates of forest transpiration can be obtained by using the HTO method to measure Q values for a few trees under the conditions of measurement, then using equation (8) to calculate the transpiration rate of all other trees of the same species during the same period. When average values of transpiration rates for the forest have been obtained, equation (5) can be used to resolve day-to-day variations in transpiration rate.

Tritium distribution in the trees

Cores of wood were taken from the Oregon tree at heights of 20, 30, 40 and 50 m on the

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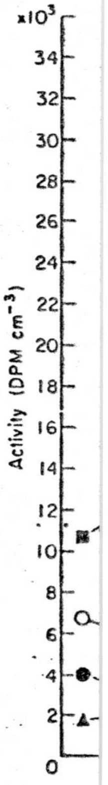

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tenth day following injection when the tritium pulse was passing through the tree. The cores were sectioned into 2-cm-long segments and analysed for HTO using a Packard Tritium oxidizer. The pulse was centred near the 40-m level at the time of sampling (Fig. 4), but extended from 30 to 50 m depending on depth of sampling in the tree

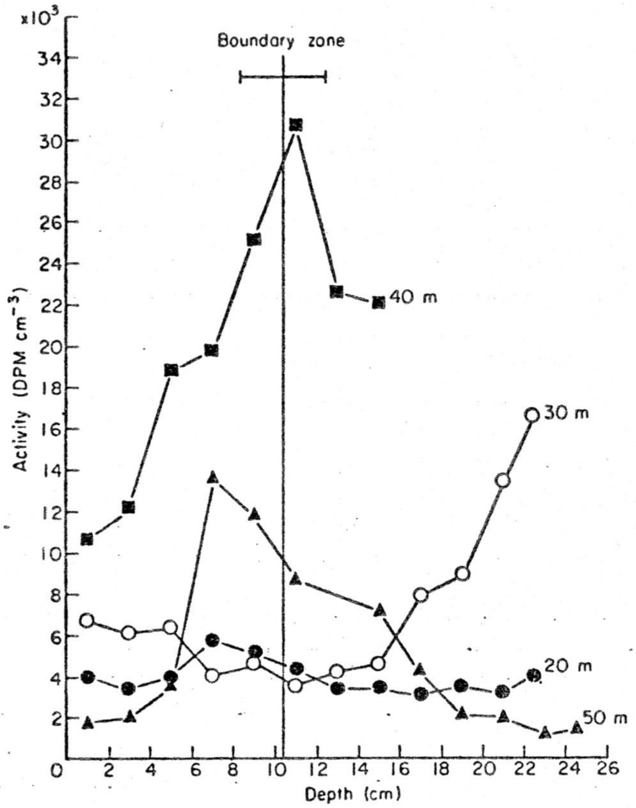

FIG. 4. The distribution of HTO in wood of the Oregon tree as a function of height (m) and depth (cm) of the cores. The boundary zone is the zone of separation between heartwood and sapwood. The indicated error interval for the zone is ± 1 standard error.

This longitudinal dispersion of HTO suggests that a wide range of different conducting pathways exists in the sapwood. In diffuse porous wood, individual conducting elements are relatively short in length and are strongly interconnected with one another (Zimmerman & Brown 1971). The interconnections progress generally in an upward direction but may follow an extremely tortuous pathway. Thus the flow of water in the tree is made up of flows with varying path lengths. The HTO which had reached 50 m had presumably followed a less tortuous pathway than that which had reached 40 or 30 m.

The mean transit time for HTO, i.e. the time required for the tritium pulse to reach peak activity in the twigs (see Fig. 1), was essentially the same at all heights of the tree. This surprising result indicates either that the pathways leading to high branches are less tortuous than those leading to low branches, or that the flow velocities leading to high branches are higher than those leading to low branches. Both explanations are possible. Because most solar radiation is absorbed in the upper part of the canopy, most water will be transpired there. Consequently, flow velocities may be higher in the upper part of the canopy because relatively large volumes of water are flowing in conduits of comparatively small cross-sectional area.

The sapwood in the tree was 10·4±2 cm thick. A considerable amount of HTO had diffused into the heartwood (Fig. 4), even though the heartwood is non-conducting. It is evident that there had been exchange of water between the heartwood and sapwood, and Ritchie & Hinckley (1971) have suggested that heartwood may serve as a reservoir of water for the plant.

The highest activity of HTO in cross-section occurs at the boundary of the heartwood and sapwood. Regions of high HTO concentration, in an actively flowing system, indicate regions of relatively low dilution with incoming water, while regions of low concentration indicate more rapid dilution with fresh water. Thus it seems that the inner sapwood has the largest resistance to water flow or the greatest tortuosity. This may occur because of the age of the inner sapwood and its imminent conversion to heartwood. The activity gradients shown from outside to inside the tree (Fig. 4) indicate that most water moves in the outer sapwood and least in the inner sapwood.

Exchange of foliar and atmospheric water

Plants which transpire tritiated water have lower concentrations of HTO in their foliage than in their source water (Raney & Vaadia 1965; Kline *et al.* 1971, 1972b). Raney & Vaadia attributed the observed deficiency of HTO in leaf water to dilution by vapour exchange of water molecules between leaves and the atmosphere. The degree of vapour exchange can be measured, in HTO labelled trees in the field, as the ratio of HTO activity in leaves to that in stems of samples collected at the same time, on the assumption that the stems are isolated from vapour exchange with the atmosphere. This is a reasonable assumption since Raney & Vaadia found that HTO activity in the stems of plants exceeded 97% of the activity of the source water in a relatively short time.

Values of the ratio of needle:twig HTO activity ranged from 0·49 to 0·81 with an average of 0·69 (Table 3). None of the ratios approached unity. The observed ratios suggest that during the period of this experiment an average of 31% of the water in foliage was of atmospheric origin rather than of soil water origin. It is not implied that this represents net uptake of water from the atmosphere but only that atmospheric water exchanged with water in the leaf by molecular diffusion. Consequently, HTO activity in leaves cannot be used to calculate the rate of transpiration. The flow resulting from

Table 3. *Ratio of HTO activities in needles and twigs of Douglas-fir in Orgeon at various dates*

Date	Activity ratio of needles and twigs (N/T)	Mean daily temperature (° C)	Mean daily saturation deficit (mb)	Mean daily transpiration rate $(\mathrm{l\ h^{-1}})$
28 June 72	0·56	24	11·9	23·9
29 June 72	0·49	24	15·2	23·2
30 June 72	0·67	22	11·1	18·4
14 July 72	0·58	25	15·2	23·4
15 July 72	0·81	27	18·2	27·6
17 July 72	0·81	29	23·2	34·0
19 July 72	0·79	22	16·1	24·0
21 July 72	0·74	21	13·4	18·0

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transpiration alone must be obtained from HTO activity in twigs since the twigs have negligible vapour exchange between xylem water and the atmosphere.

Error in transpiration measurements

If HTO from an input pulse is well mixed in the tree by the time it is transpired, the sampling error is low. In practice, composite samples were taken from several parts of the canopy at each sampling time to minimize sampling error. However, samples from the Oregon tree were collected separately and the standard error of the mean at each height was computed for each sampling time. The error was substantial early in the experiment (Fig. 5) but diminished rapidly to a fairly steady value after ten days. The large early error had little effect on estimates of transpiration, since most of the area under the activity-time curve occurred after the time of peak activity, when the error had reached its minimum value. The standard error of the area beneath the activity-time curve, using the method of Kline *et al.* (1970), was less than 10% for all trees.

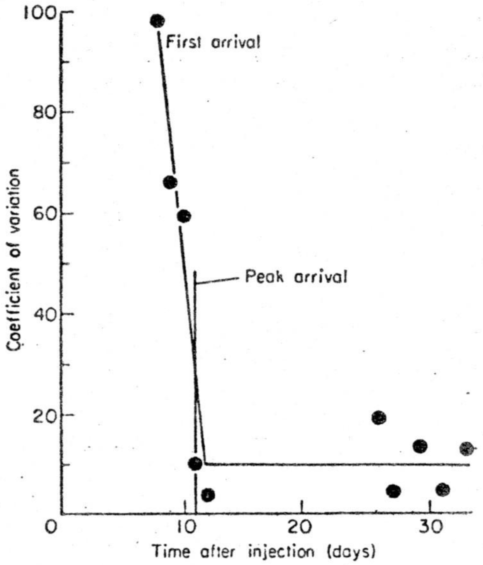

FIG. 5. Changes in the coefficient of variation of HTO measurements in the Oregon tree with time.

CONCLUSIONS

In forests with a single dominant species a reliable estimate of whole forest transpiration, on a daily basis, could be obtained from HTO tracer measurements on eight to ten trees distributed over the full size range. From each tree, 25–35 composite twig samples are required for a complete description of the activity-time curve. Thus the transpiration rate of a forest could be found from the analysis of HTO in approximately three hundred plant samples. This is quite practical, since it is feasible to analyse fifty samples per day. Measurements of net radiation, air temperature and dew point temperature are required to estimate transpiration on a daily basis, and radii of heartwood and sapwood of all trees in the area are required to extrapolate to trees of different sizes.

It is concluded from the present studies that the HTO tracer method is a reliable and practical means for measuring forest transpiration.

ACKNOWLEDGMENTS

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SUMMARY

(1) Transpiration rates of Douglas-fir trees (*Pseudotsuga menziesii*) were measured in the field, using tritiated water (HTO) as a tracer for water. Sites were located in the Cedar River Watershed near Seattle, Washington and in the Andrews Experimental Forest near Eugene, Oregon.

(2) Transpiration rates ranged from 8·4 l day^{-1} in a small tree to 530 l day^{-1} in a large old-growth tree on the Oregon site.

(3) A relationship between transpiration rate and sapwood cross-sectional area of trees was found which would permit extension of individual tree measurements to forest populations.

(4) The HTO measurements, linked to current physical theories of evapotranspiration, permit the computation of actual daily transpiration rates for individual trees or areas of forest.

(5) The method allows direct measurements of water loss from forests in situations where lysimeter installation would be impractical.

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c	cal gm^1 ° C^{-1}	spe
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A	cm^2	cro
R_t	cm	rad
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APPENDIX A

Definition of mathematical symbols

F	cm^3 hr^1	flow rate of trees as computed by the Stewart-Hamilton equation
F_i	cm^3 hr^1	actual daily flow of trees averaged over 24 h
$\bar{F}$	cm^3 hr^1	mean flow rate of trees averaged over entire experimental period
M	DPM	total amount of HTO injected into a tree for a transpiration measurement
t	hr	time
T_i	cm sec^{-1}	transpiration rate given by solution of Montieth's equation which is averaged over 24 h
T	cm sec^{-1}	transpiration rate given by solution of Montieth's equation which is averaged over the full experimental period
R_n, $\bar{R}_n$	cal cm^{-2}sec^{-1}	net solar radiation, daily and extended averages
S,$\bar{S}$	m bar ° C^{-1}	change of saturation vapour pressure with temperature; daily and extended averages
ρ	gm cm^{-3}	density of air
c	cal gm^1 ° C^{-1}	specific heat of air
λ	cal cm^{-3}	latent heat of vapourization of water
Y	m bar ° C^{-1}	psychrometric constant
e_s,$\bar{e}_s$	m bar	vapour pressure of water in the atmosphere at saturation; daily and extended averages
e, $\bar{e}$	m bar	vapour pressure of water in the atmosphere; daily and extended averages
r_a,$\bar{r}_a$	sec/cm	external forest resistance; daily and extended averages
r_s,$\bar{r}_s$	sec/cm	stomatal resistance; daily and extended averages
Q	cm hr^{-1}	velocity of sapflow through xylem of trees
A	cm^2	cross-section of sapwood
R_t	cm	radius of tree inside bark
R_H	cm	radius of heartwood