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DIRECT MEASUREMENT OF TRANSPIRATION AND BIOMASS IN CONIFEROUS TREES

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INTRODUCTION

This is a final report to the Coniferous Forest Biome of the U.S. International Biological Program concerning research on forest transpiration and biomass measurement that was performed under ANL proposal P-7103 A to the Biome during the period January - December 1972.

Measurement of transpiration rates and biomass of Douglas-fir (*Pseudotsuga menziesii*) was performed in the field at the Cedar River watershed site near Seattle, Washington and at the Andrews Experimental Forest near Corvallis, Oregon. The method employed for these measurements was based on the use of tritiated water (HTO) as a tracer for water. The use of HTO for such measurements has been demonstrated by Kline, et al. (1970, 1971, 1972a, 1972b) in other forests. Tracer methodology which was employed is based on the theory of tracer dynamics which has been discussed extensively by others for the measurement of *in vivo* kinetics of biological systems; Bergner (1961, 1964a, 1964b, 1965, 1966), Zierler (1964), Orr and Gilespie (1968), Ljunggren (1967), Shipley and Clark (1972). The theory of tracer dynamics has been used to measure flow rates in such diverse systems as rivers, industrial processes and blood flow in organisms. It has not been used previously except by us for the determination of transpiration flow in plants.

The objectives of this study were: (1) to measure the water consumption rates and the biomass of Douglas-fir in the field for the purpose of obtaining a basic data set which could be used as input to the biome hydrological and biomass modeling effort as well as for input to other modeling efforts carried out by the authors, (2) to extend the range of experience with the techniques beyond past limits and to verify as much as possible their generality of application, (3) to compare transpiration measured by the HTO method with values calculated from meteorological measurements, (4) to develop new methods for extending single-tree HTO methods for transpiration measurements to whole forest areas and improve their resolutions in time, and (5) to confirm the validity of nondestructive biomass measurement with the HTO method over a larger range of tree sizes than has previously been done.

MATERIALS AND METHODS

Transpiration rates in Douglas-fir were measured with the tritium (HTO) method at the University of Washington research site on the Cedar River watershed and at the Oregon State University experimental site on the Andrews Experimental Forest. A total of ten trees were injected with HTO at the Cedar River site and one large old growth tree was injected on the Andrews site. Table 1 shows the organization of the experiments and the amount of tritium used in each.

Tritiated water was transported to the experimental sites in sealed medical serum bottles. Injections were accomplished by withdrawing a known volume of HTO from the vial with a precalibrated hypodermic syringe and injecting it into holes which had been bored into the base of the trees.

The holes were bored immediately prior to injection and were sealed immediately afterward to prevent the escape of HTO. The injection holes were bored with a one-eighth-inch twist drill or small increment borer and were evenly spaced around the base of the trees. The number of holes used for injection range from 4 on the smallest trees to 20 on the largest. All injections went directly into the sapwood of the trees. The injection holes did not extend into heartwood.

The HTO solutions used for the injection were precalibrated for radioactivity at Argonne National Laboratory. The calibrations were accomplished by comparison of the count rates of the experimental solutions with the rates of commerical standard solutions using a liquid scintillation counter. Corrections for quenching and background were made for all samples. The units of radioactivity used for the standards and all experimental samples were DPM/ml (disintegrations per minute per ml). Corrections for radioactive decay were not made on samples collected during the experiment because of the long half-life of tritium (12.3 yr).

After injection, the trees were sampled once or more daily until HTO had passed completely through the tree. Sampling was accomplished by shooting branches from the trees with a shotgun in most cases, although climbers collected some samples from the old-growth tree on the Andrews experimental forest. Sample collection by climbers was too expensive to be pursued on a prolonged basis and this method was abandoned. The shotgun method of collection was completely satisfactory and sufficiently economical to be used on a sustained basis.

At each sampling time, twigs and needles were collected from several parts of the canopy and were combined to provide a sample for analysis. The samples were placed in plastic bags for storage and were frozen as soon as possible after collection to prevent the loss of tritium. Leaves and twigs were separated prior to combining and twigs were used as the primary source of data for the computation of transpiration rates of trees.

The samples were sent to Argonne National Laboratory for analysis. The analysis was accomplished by freeze drying the samples and counting the water recovered in this process by liquid scintillation methods. The freeze-dry procedure has been described by Stewart, et al. (1972). Briefly it consists of removal of the water from the samples in a custom fabricated manifold apparatus which can be evacuated to less than 10 microns pressure with a vacuum pump. When the sample has been evacuated one end of the glass sample container is imbedded in dry ice while the other remains in room temperature. Water from the sample migrates from the warm to the cold end of the container and freezes there. After an overnight run the container is disassembled and the ice is allowed to melt. The water which has been recovered is pipetted into a commercially prepared liquid scintillation cocktail in preparation for counting. The freeze-dry process results in water removal from plant sample to the equivalent of oven dryness after about 12 hours. About 50 samples per day can be processed with this apparatus.

The samples were counted in a Packard Tri-Carb liquid scintillation counter. Data were corrected for quenching and background and were expressed as DPM/ml. The data were plotted on rectangular coordinates as a function of time to provide the activity-time curve needed for the computation of transpiration rates and biomass.

At the termination of the experiments, eight trees on the Cedar River site were cut and weighed to provide independent estimates of biomass for comparison with the HTO method for estimating biomass. The cut trees were separated into components of branches, leaves, and bole although the HTO method does not permit this resolution. At the time of cutting, samples were also collected for plant moisture determination. At this writing the biomass of the experimental tree in the Andrews forest has been estimated only by an independent nondestructive method. Present plans call for felling and weighing this tree sometime during the summer of 1973.

The experiments were carried out on the Cedar River site near the location of the lysimeter tree and its associated meteorological instrumentation. This was done to permit confirmation of the HTO derived data by independent methods of calculating or observing transpiration rates. The tree on the Andrews site in Oregon was near the location of an automated climatological station which recorded solar radiation, air temperature and dewpoint temperature. These weather records were used to make auxilliary computations of transpiration rates in the forest.

At the time of this writing, data from the Cedar River lysimeter installation were not available. This report was prepared without these data in the interest of rapid dissemination of information to the Biome. When new data are available which permit comparison of HTO and lysimeter transpiration rates they will be included in a supplementary report to the Biome.

RESULTS

Transpiration

After injection of the trees with HTO, samples of twigs were collected until the radioactive pulse had passed completely through the system. Specific activity of HTO in the twigs was plotted as a function of time yielding a characteristic curve known as the activity-time curve. An example of an activity-time curve is given in Figure 1.

Transpiration rates of all trees were calculated from their individual curves of specific activity *vs.* time using the Stewart-Hamilton equation

$$M = F \int_0^\infty f(t)\,dt \qquad (1)$$

(Definition of all mathematical symbols is given in appendix A).

In this equation the value of the integral is simply the area under the activity-time curve. The equation states that the total activity in the system is given by the product of the flow rate through it and the total area of the activity-time curve. In this equation all quanitities are known except flow (F). This is solved for algebraically. The value of F given by the equation is the average value that would be obtained if the tree transpired at a constant rate during both day and night.

Transpiration rates obtained using HTO tracer and equation (1) are given in Table 2 for ten experimental trees on the Cedar River watershed and for one large old-growth tree in the Andrews Experimental Forest in Oregon. Two estimates of transpiration are given for each of the Cedar River trees. This is because the transpiration conditions during these experiments were not constant and special techniques were needed to obtain the estimates.

During the experiments with trees 2-10 at the Cedar River site a week of heavy rainfall occurred after the transpiration experiment had been in operation for eight days. At the end of the rainy period sampling was resumed to complete the construction of the activity-time curve. The activity-time curves had passed their peak activity before the rain and HTO activity was well down on the descending branch of the curves when the rain started. This made it possible to estimate both the average transpiration rate during sunny weather and the average rate during the combined sunny and rainy weather. The sunny weather estimate was obtained by extrapolating the curves on semilogarithmic coordinates with the same slope that was established prior to the rainfall and integrating the resulting activity-time curve. The combined sunny and rainy weather average was obtained by integrating the actual curve during the full period of the experiment which included the rainy period. Figure 1 shows a typical curve that was obtained during this experiment and the extrapolation that was made in order to estimate the sunny weather transpiration rates.

The experiment with tree number 1, done earlier in the summer, was also interupted by rainfall. In this case the rain began immediately after injection of the HTO solution and it persisted for a week. This was followed by a period of sunny weather which lasted long enough to permit the HTO to be completely passed through the tree. The activity-time curve showed the period of zero transpiration as a long constant activity portion of the curve. When transpiration resumed, the specific activity in the tree changed rapidly as a function of time and a normal response curve was obtained. In this case most of the measured transpiration was that which took place after the rain and it was not possible to resolve the curve into two parts by extrapolation. The method for calculating transpiration in this tree is given in Appendix B.

The experiment in Oregon was performed with significant interruption by rainfall and the transpiration rate was calculated from the full observed curve without extrapolation or other special techniques.

Daily Average Transpiration

The transpiration rates shown in Table 2 are average rates for either the full term of the experiments or for the sunny weather portion of the experiments. The Stewart-Hamilton equation as written does not permit resolution of the extended average rate into actual daily averages. Indeed the equation is derived under the assumption that the flow to be measured is constant during the measurement period. This is the principal of "stationarity" which was expressed by Zeirler (1964). As was pointed out by Orr and Gilespie (1968), however, the equation is not very sensitive to deviations from the constancy of flow assumption and the equation can be used validly in systems where it is not strictly true. We (Kline, et al. 1971) have examined the case for trees in which the flow ceases or slows sharply at night and resumes again in the daytime and found that this does not violate the "stationarity" principal. Applying the equation, however, results in an estimate of flow which is essentially averaged over periods of rainfall and sunshine, periods of night and day and over other variations which normally occur during any experimental period. There is no apparent way to improve the resolution of actual day-to-day flow rates without auxilliary data.

When climatic data are available, however, it has been found feasible to resolve the long term average flow rates into daily averages. This was done using the version of Montieth's equation for transpiration which was given by Rutter (1968). Montieth's equation is given as equation 2.

$$T_i = \frac{S\ R_n + \rho c\ (e_s - e)/r_a}{\lambda s + \lambda y\ [(r_a + r_s)/r_a]} \qquad (2)$$

The average flow rate for the entire period is also given by the Montieth's equation in which all the variables are averaged for the period of the experiment. This is shown by equation (3).

$$\bar{T} + \frac{\bar{S}\ \bar{R}_n + \rho c\ (\bar{e}_s - \bar{e})/r_a}{\lambda\bar{S} + \lambda y\ [(r_a + \bar{r}_s)/r_a]} \qquad (3)$$

In the usual application of Montieth's equation, transpiration is calculated in an absolute manner from the climatic variables. It is proposed that when mean flow rates are known from the HTO experiments, these equations can be used to make a relative calculation which should be more accurate than direct evaluation of equation (2). This is shown by equation (4) in which it is assumed that actual transpiration is proportional to the rate which is computed with the Montieth equation.

$$F_i/T_i = \bar{F}/\bar{T} \qquad (4)$$

Substituting equation (2) and (3) into (4) we obtain a final expression for mean daily transpiration rate [equation (5)]:

$$F_i = \bar{F}\ \left[\left[\frac{S\ R_n + \rho c\ [(e_s - e)/r_a]}{\bar{S}\ \bar{R}_n + \rho c\ [(\bar{e}_s - \bar{e})/r_a]}\right] \times \left[\frac{\bar{S} + Y/r_a(r_a + r_s)}{S + Y/r_a(r_a + r_s)}\right]\right] \qquad (5)$$

If soil moisture stress is not variable during the period of the experiment it can be assumed that: $r_s/\bar{r}_s = 1$. The ratio involving stomatal resistances in equation (5) then cancels approximately. When the stomatal resistance terms cancel, the remaining expression states that daily transpiration rate is principally a function of net radiation and saturation deficit. These terms are easily measurable in forest and are often available.

Equation (5) was evaluated for the Oregon tree over a period of 34 days during which the overall mean transpiration rate was found to be 22.1 liters hour^{-1}. The evaluation was performed under the assumption of constancy of stomatal resistance. The results are shown in Figure 2. Data required for the computation are given in Appendix C. The results shown are average rates for a 24-hour day. This calculation could be made equally well for individual trees or for an entire forest. In theory it should be more accurate than an absolute evaluation of Montieth's equation because many systematic errors in measurement of climatic variables will cancel exactly in the ratio of equation (5). Also, many site-specific variables not specifically included in Montieth's equation will cancel out in the ratio if the calculation is made for the site which the HTO experiments were performed. The sensitivity analysis of Table 3 demonstrates the stability of the ratio against error in some variables.

Any equation purporting to be descriptive of transpiration could be used in place of Montieth's equation in equation (5). It is not required that the equation used be exactly description of transpiration. The principal requirement for the ratio method is that the true transpiration rates be proportional to the rate given by whatever equation is used. The equation given by Waring, et al. (1973), for example, would be well suited for substitution into equation (5).

Evaluation of equation (5) may be viewed as a process of allocation of a known total volume of water to the individual days which vary in their evaporative potential during the experimental time interval. Regardless of how the water is allocated with this equation, the average transpiration rate after allocation is the same as the overall grand average which is obtained in the HTO experiment. The evaporative conditions on any given day may not vary by more than a factor of 2 or 3 from the average conditions of the experiment. Because of the allocation feature the experiment may be done under conditions of either high or low soil moisture stress, even though most transpiration equations are valid only for conditions in which actual transpiration is equal to potential. The main limitation to the ratio method occurs in the assumption that stomatal resistances are constant during the experimental period. Errors in the computed result will occur from the failure of the stomatal resistance terms to cancel in equation (5) if this assumption is not met. The actual value of stomatal resistance however is not important. The allocation can be done whether the value is high or low during any period in which the constancy assumption is valid.

Equation (5) could be solved without any assumptions about stomatal resistance if some easily measured variable which was proportional to that quantity could be found. If for example predawn plant moisture potentials were measured concurrently with an HTO experiment they might at least reveal when the constancy assumption was invalid but might also be used as a proportional variable to solve equation (5) more exactly.

Transpiration measurement by the HTO method enables the computation of daily average flow rate by a process based on the use of a dimensionless ratio. Use of the ratio requires no unrealistic assumptions or approximations. The expressions used in the ratio are those which ordinarily are used to make absolute estimates of transpiration rates. Because the value of the ratio is highly resistant to change when the input variables change, it is concluded that the ratio method permits the computation of daily average transpiration rates which are limited in accuracy primarily by the averages obtained in the HTO experiments when stomatal resistance are constant.

Conductivity Measurements

In a flowing system the flux of water through the system is equal to the product of the velocity of flow and the cross section as shown by equation (6).

$$F = QA \tag{6}$$

The conducting cross section of a tree is equal to the cross section of the sapwood since the heartwood is known to be nonconducting. The cross sectional area of sapwood is given by equation (7).

$$A = \Pi \, (R^2{}_t - R^2{}_h) \tag{7}$$

Substituting (7) into (6) results in equation (8).

$$F = Q \, \Pi \, (R^2{}_t - R^2{}_h) \tag{8}$$

A graph of F *vs.* $\Pi \, (R^2{}_t - R^2{}_h)$ should yield a straight line on rectangular coordinates with intercept of zero and slope Q. The value of Q may be regarded as the specific conductivity of the sapwood in dimensions of $cm^3/hr - cm^2$, or more simply as the velocity of flow in units of cm/hr.

Measured values of transpiration were plotted against sapwood cross section for the Seattle trees and the results are presented in Figure 3. The regression equations for the relationships are given in Table 4. The correlation among the Seattle data is highly significant with a coefficient of determination (r^2) value of 0.954. The intercept was 0.21 as compared with an expected value of zero and the slope was 5.71 cm/hr. The large old-growth tree from Oregon which was measured at a different time and place had an individual Q value of 5.54 cm/hr. This value fits the regression line established for Seattle trees and in fact improves the significance of the correlation. The data suggest that average sap flow velocities are quite constant among individuals of the same species over a wide range of sizes and even at different locations. All of these measurements however were made under conditions of low soil moisture stress and may be maximum values for the species. The values may change as the stress increases. Some daily values of conductivity are given in Appendix C.

Sapflow velocities measured by the tritium method agree well with values for Douglas-fir saplings which were obtained by Hinckley and Scott (1971) and by Hinckley (1971) using a thermoelectric sap velocity meter. Hinckley and Scott's values range from 4.2 to 6.2 cm/hr when averaged over several days. Differences among trees in their experiments were apparently due to different xylem sap pressures. The agreement suggests that sap velocity measurements 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 show a considerable sap velocity persisting during periods when transpiration approaches zero. It is not clear why this is the case, however, it suggests that errors will result if too great a resolution of transpiration rates are attempted using the thermoelectric method. On the other hand our time average values agree well with the published time average values obtained with the sap velocity meter. It is these values which we suggest may be useful to calculate transpiration with equation (8).

Hinckley's comment that others had found a decreasing correlation between sap flow or transpiration and increasing stem diameter is understandable in the light of the present data. We would not expect stem diameter to be the appropriate variable with which to attempt the correlation. As has been shown, transpiration and sap velocity are strongly related to sapwood cross section and not stem diameter over a wide range of tree sizes.

Reasonable estimates of forest transpiration could be obtained using the HTO method for measurement of transpiration and Q values for a few trees in the forest. These measurements could be utilized to essentially "calibrate" the forest under the conditions of measurement and would permit the use of equation (8) to calculate the transpiration rate of all other trees of the same species during the same period. When average transpiration values for the forest had been obtained, the use of equation (5) to resolve day-to-day transpiration would permit a detailed resolution of this process which could not be obtained using any other known field measurement except lysmetry.

The apparent constancy of conductivity in Douglas-fir sapwood among individuals measured under similar conditions has implications concerning the relationship between size of trees and the maximum plant population density which can be accommodated in climatic regime. A sample calculation will illustrate.

Suppose that the time average potential transpiration for a region is 5 mm/day, and that water supply is not limiting. This is equivalent to flux of 0.5×10^8 cm^3/day-hr. This amount of water must pass through a conducting medium having a conductivity of 5.7 cm^3/hr-cm^2 or 136.8 cm^3/day-cm^2. The forest may therefore be limited to a maximum of $0.5 \times 10^8/136.8 = 0.368 \times 10^6$ cm^2 of conducting tissue per hectare.

If the forest is old and consists of trees as large as the Oregon experimental tree which had a cross sectional area of sapwood of 4×10^3 cm^2 then it is apparent that there should be about $0.368 \times 10^6/4 \times 10^3 = 91$ trees per hectare of this size. For a forest having an average conducting cross section of 1000 cm^2/tree a population of 368 trees per hectare could be sustained. It would be a simple matter to improve these calculations and to experimentally verify the dependence of tree population on potential transpiration.

There exists a strong relationship between conducting cross section and leaf biomass among the Cedar River experimental trees (Figure 4). The correlation is linear and has a coefficient of determination (r^2) value of 0.91. The correlation equation is given in Table 4. The relationship suggests that leaf biomass is limited by the ability of the plant to supply water to the leaves. The conducting cross section and the conductivity of the sapwood may combine to place an upper limit on the possible amount of leaf biomass on any one tree. It is widely believed that degree of cover is the primary variable limiting plant population density. This is probably true but it now appears that cover and leaf biomass may itself be limited by the conducting capability of the sapwood.

Tritium Distribution in Trees

Cores of wood were taken from the Oregon tree at 20, 30, 40, and 50 meters above the ground during the time the tritium pulse was passing through the tree. The cores were sectioned into 2-cm segments and analysis for HTO was performed on each using a Packard Tritium oxidizer. The distribution of HTO in the tree at the time of coring is shown in Figure 5. The data show a high degree of longitudinal dispersion of the tritium pulse in the tree. The pulse was centered near the 40-meter level in the tree at the time of sampling, however, it extends back to 30 meters and upward to 50 suggesting that the pulse has a base width of 20 meters. This dispersion was produced during the time when the net upward movement of the peak was only 40 meters.

The longitudinal dispersion of HTO suggests the existence of a wide range of different conducting pathways in the sapwood. The xylem of difuse porous species has been described by Zimmerman (1971). Individual conducting elements are relatively short in length and are strongly interconnected with one another. The interconnections progress generally in an upward direction but may follow an extremely torturous pathway. Thus the flow in the tree is not uniform but a distribution or family of flows with varying path lengths. The HTO which had reached 50 meters had followed a less torturous (shorter) pathway than that which had reached 40 meters during the same time. Similarly the HTO at 30 meters had followed a longer more torturous pathway than that at 40 meters.

The pathways followed by water in the xylem are not without order however. This is indicated in Table 5 where it is shown that the mean transit time for HTO was essentially the same at all levels of the tree. The mean transit time or mean residence time is the time required for the tritium pulse to reach peak activity in the foliage. The surprising result that the same time is required for water to transit to any point above ground regardless of height indicates either that the pathways leading to high branches are less torturous than those leading to low or that the flow velocities leading to high branches are greater than those leading to low. There seems to be no mechanism which could account for variation in flow velocity. The differences in apparent velocity are easily accounted for by differences in tortuosity or path length however. In Table 5 we calculate the relative path length or tortuosity of all levels in the tree in relation to that at the 20-meter level. The relative path length of 0.5 for the 40-meter level indicates that the pathway of water to that level is only half as tortuous as that at the 20-meter level.

It should also be noted from Table 5 that the apparent velocities are much greater than 5.7 cm/hr which was the average at ground level for the tree as a whole. This indicates that the velocity of sapflow is dependent on where it is measured. Due to the normal taper of the tree it would be expected that the over all velocity would increase with height above ground.

The distribution of HTO in the cross section of the large Oregon tree is shown at several levels in Figure 6. In this tree the sapwood was 10.4 ± 2 cm thick. The data show that a considerable amount of HTO had diffused into the heartwood. Even though the heartwood is non-conducting it is evident that there is dynamic exchange of water between the heartwood and sapwood. The heartwood is not hydraulically isolated from the sapwood. This is consistent with the conclusion of Ritchie and Hinckley (1971) who 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. This suggests that the inner sapwood has the greatest resistance of water flow and therefore 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 indicates that the greatest conduction of water occurs in the outer sapwood. The lower HTO activity there is due to greater dilution with incoming fresh water. Regions of low activity indicate regions of high water flux in the sapwood.

At the heartwood-sapwood boundary there is a diffusion gradient of HTO into the heartwood. At the 30-meter level, for example, it appears that the sapwood was emptied of HTO by new water and that the heartwood was returning its burden of HTO to the sapwood by diffusion. At the 40-meter level it may be that the heartwood was still acquiring a label by diffusion since the gradient is inward towards the center of the tree. Similarly at the 50-meter level, the maximum activity occurs near the boundary and diffusion gradients exists from the maximum into both the heartwood and the sapwood.

It is concluded that differential flow rates take place across the sapwood and that the inner sapwood conducts more slowly than the outer. We further conclude that the differences in apparent velocity are controlled by tortuosity of the conducting medium and that the faster apparent velocities are due to the existence of shorter path lengths for the water to pass through. If this hypothesis is correct it follows that the old low branches are supplied with water from the oldest (inner) sapwood and that the younger be the reason for the commonly occurring self pruning of branches which takes place in conifers. The oldest low branches are supplied with water from the oldest sapwood. As this wood is converted to heartwood these branches necessarily lose progressively more of their water supply until they finally die.

Exchange of Foliar and Atmospheric Water

It was demonstrated by Raney and Vaadia (1965) that plants which are transpiring tritiated water have lower concentrations of HTO in their foliage than there is in their source water. We (Kline, et al. 1971, 1972a) have also observed this in the field in both grasses and trees and have found that equivalence between activity in foliage and that in the source water is never achieved regardless of how long the experiment is prolonged. Raney and Vaadia attributed the observed deficiency of HTO in leaf water to exchange of water molecules between leaves and the atmosphere. This has been termed "vapor exchange." Vapor exchange between leaves and atmosphere occurs in all plants which have been observed thus far. This includes conifers, broad leaf tree, succulent forbs, and grasses. The degree of vapor exchange can be measured in HTO-labeled trees in the field by the ratio of activity in leaves and stems of samples collected at the same time. This is done under the assumption that the stems are hydraulically isolated from the atmosphere. This is a reasonably reliable assumption since Raney and Vaadia found that the stems of plants achieved in excess of 97% of the activity of the source water in a relatively short time.

Needle-twig activity ratios are given for the Oregon tree in Table 6. The values of the ratio range from 0.49 to 0.81 and have an average of 0.69. None of the observations approach or reach one. The observed values 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 vigorously exchanges with leaf water. There is no other apparent explanation for the reduction of HTO activity in leaves. Such a reduction can only take place by exchange or dilution with untritiated water.

The actual concentration of HTO in leaves is the result of both the exchange rate and the rate of delivery of fresh tritiated water to the leaves. The exchange rate and the delivery rate are both dependent on atmospheric moisture but no mathematical expression has yet been found which describes the process. It is not yet clear whether the uptake of atmospheric water has any physiological benefit to the plant or whether a net uptake could occur under some conditions. The substantial fraction of leaf water which originates from the atmosphere suggests that this phenomenon is worth investigating further to determine its relative significance in plant water relations.

Error in Transpiration Measurements

Statistical error in transpiration measurement arises from sampling variance. If HTO from an input pulse is well mixed in the tree by the time it exits then the sampling error will be low. If it is poorly mixed the sampling error is large. In practice composite samples are taken from several parts of the canopy at each sampling time, in order to minimize sampling error as much as possible.

In the very large Oregon tree composite samples were collected separately from the 20-, 30-, 40-, and 50-meter levels, and the standard error of the mean was computed for each sampling time. The percent standard error was plotted as a function of time for the experiment. The results are given in Figure 7. They show that there was substantial mixing error early in the experiment but that this error diminished rapidly to an average value of less than 10% and then remained constant for the rest of the experiment. Large statistical errors occur primarily when the activity-time curve is on its rising branch. The slope of the rising branch of these curves is so great that large errors in estimating activity have little effect on the computed area of the curve (see Figure 1). Most of the area under the activity-time curve is measured after it goes through peak activity and begins its descending branch. By the time the descent begins, the mixing error has reached its minimum value and the uncertainty in the area of the curve is a minimum. Since the area of the curve is the parameter needed for computation of transpiration, it is concluded that transpiration is known with an uncertainty of less than 10% for one standard error on the Oregon tree. Spot checks for sampling error with the Cedar River trees indicatedaa similar error level.

BIOMASS MEASUREMENTS

Biomass determinations in trees by the HTO method are based on simple compartmental dynamics for flowing systems as given by Zeirler (1964). The method utilizes the activity-time curve from the transpiration measurements to determine the water quantity of the tree. When this is known the tree biomass can be calculated from its moisture percentage. Equation (9) is the basic relationship for the determination.

$$C_v = F \times T_m \tag{9}$$

We have previously shown (Kline, et al. 1972a, 1972b) that the dry weight of the tree can be computed when the moisture percentage is known using equation (10).

$$D = F \times T_m/f \tag{10}$$

Equation (10) is used for the determination of conducting biomass of the tree. It has been found to be suitable for use as shown when the tree does not have an appreciable component of heartwood. In large trees, having heartwood, equation (10) still yields the biomass of the conducting or sapwood portion, but a correction is required to obtain the total biomass.

We have proposed a method of correcting biomass for the nonconducting or heartwood part, which is based on a geometric analysis (Kline, et al. 1972b). The correction factor when combined with equation (10) yields equation (11), which is the expression used in these experiments for calculating total above ground biomass in the experimental trees.

$$D_t = \frac{F \times T_m}{f}\left[\frac{R^2K}{\Delta R\ (2R_t + \Delta R)} + 1\right] \tag{11}$$

Determination of biomass requires more input data than transpiration measurements. In addition to flow rate and mean residence time of water several measurements on heartwood and sapwood are needed. Table 7 shows the required measurements for all trees along with other descriptive data.

Table 8 gives the biomasses for sapwood and the total biomass for each tree of the experiment along with the parameters needed to compute it. Heartwood correction values were computed from equation (11) using data from Table 7. Mean residence times were determined by the extrapolated peak arrival method which was described by Kline, et al. (1972a). The flow rates were determined by extrapolation of the activity-time curve as if the experiment had not been interrupted by rainfall before it was completed. (Table 2). Moisture content of sapwood was taken to be 114 ± 12% of all trees. The uncertainty in moisture content is the largest single source of error in biomass estimates. In future experiments considerable effort should be expended to obtain accurate moisture values.

The trees from the Cedar River site were harvested and weighed to obtain an independent estimate of biomass. The relationship between computed and observed biomass is shown in Figure 8. The regression equation for the relationship is given in Table 9. It is concluded from this data that the HTO method for biomass determination in trees is unbiased and could be used for the nondestructive measurement of biomass in the Douglas-fir forest.

In coniferous trees the radius square ($R^2{}_t$) is well correlated with biomass. A common method for determination of forest biomass is to harvest a few trees over their full size range and to plot biomass vs. $R^2{}_t$ or some other tree dimension. When the dimensions of other trees are known it is possible to estimate their biomasses from the relationship. Figure 9 shows the relationship between both calculated and measured biomass and tree radii.

The regression equations for the relationships are given in Table 9 as relationships number 3 and 4. Neither the intercepts nor slopes are significantly different from one another in these relationships. It is therefore concluded that the biomass of the forest as a whole could be determined by commonly used alometric relations in which the independent biomass estimate comes from the nondestructive HTO method rather than by direct harvest.

The Oregon tree is the largest in which nondestructive biomass measurements by the HTO mehtod have been made. At the time of this writing its biomass had not yet been measured by direct weighing. A nondestructive estimate by the method of Addor (1972) however yielded a value of 16,800 kg. The value from the HTO method was 20,130 kg. Both methods are subject to measurement error and it is not certain which, if either, is correct. The best estimate to date for this tree is therefore 18460 kg ± 9.0% (avg dev). The error in this estimate is within the range of errors which have been observed before and it is concluded that the HTO method is probably valid for estimating biomass in Douglas-fir over the full range of sizes likely to be encountered.

SUMMARY AND CONCLUSION

Transpiration rates were measured in Douglas-fir by the HTO method on both the Cedar River Watershed in Washington and the Andrews Experimental Forest in Oregon. New results from these studies show that transpiration rate for Douglas Fir is strongly related to the conducting cross sectional area of the sapwood. The relationship has enabled the computation of specific conductivity for the wood which in simpler units is simply the sap flow velocity. Values derived by the HTO method agree well with those from the thermoelectric method and suggest the validity of transporation measurements using tritiated water. Measured average conductivity values were the same whether measured in the Washington trees or the Oregon tree suggesting that conductivity is characteristic for this species.

It now appears feasible to measure transpiration for an entire watershed with the HTO method by measuring a few trees of each species in a forest over the full size range in which they occur. Using the conductivity relationships which have been found it becomes possible to compute transpiration rates for all trees when their sapwood cross sections are known. Thus there exists a new allometric relationship in which water consumption rather than biomass is calculated from knowledge of tree dimensions.

The conductivity relationship has biological implications which require further exploration. The apparent characteristic conductivity of the sapwood suggests the possibility that the forest may adjust the amount of sapwood per unit area for the average potential transpiration of the region. If this hypothesis is correct it would be expected that the cross sectional area of sapwood per unit area of forest would be fairly constant for forests differing in average tree size. Constancy of conducting cross section could be maintained both by regulating plant population and by conversion of sapwood to heartwood in existing trees as they increase in size. The commonly observed decrease in population with increasing tree size and age is consistent with this hypothesis. A simple test of this hypothesis could be obtained by measuring the sapwood cross section per unit area for forests in different stages of growth to determine whether this factor is constant among forests.

The amount of leaf biomass per tree appears to be regulated also by the conducting cross section. There can be no more leaves on a tree than can be supported by its water conducting capability. This also suggests that plant population density is regulated at least to some extent by water conducting capability. While it is undoubtedly true that the immediate regulator of population density is plant cover it now appears that the cover itself is regulated by conductivity of active xylem.

Transpiration results given by the Stewart-Hamilton equation in a tracer experiment are not resolved in time. The equation yields an extended time average estimate of transpiration rates over an interval which may range from a few days to several weeks. Detailed resolution of transpiration rates into actual daily averages is possible, however when the extended average measurements are combined with equations describing transpiration such as those of Penman or Montieth. Such a combination permits the computation of average daily flow rates from a dimensionless ratio and the extended average rate. The computation is a relative one instead of an absolute estimate which is obtained by direct solution of the transpiration equations. The relative estimate is highly resistant to error or change when the input data is in error. The estimates are therefore expected to be a more reliable than those obtained by absolute calculation from climatic variables alone.

When the relative method for computing actual daily transpiration is combined with the computation of forest transpiration from cross section of sapwood it becomes possible to obtain water consumption rates for an entire forest with a high degree of resolution in time. This information is obtainable with relatively little effort considering the importance of the results.

In forests with a single dominant species a reliable estimate of whole forest transpiration on a daily basis could be obtained from 8-10 trees which were selected over the full size range in which they occur. Each tree requires 25-35 composite twig samples for complete description of its activity-time curve. Thus the information described above could be obtained from a forest throughthe analysis of approximately 300 tritiated plant samples. Since it is feasible to analyse 50 such samples per day it is evident that no undue effort is involved for the tracer phase of describing forest hydrology.

The computation would require additionally the measurement of net radiation, temperature and dew point temperature as well as radii of heartwood and sapwood of all trees in the forest. The moisture content of sapwood and the heartwood and sapwood densities would also be required if biomass estimates were to be made.

Biomass determinations in trees by the HTO method were well correlated with values obtained by harvest. It was shown that allometric relationships which predict tree biomass from some dimensional parameter such as the radius square were equally reliable whether the independently measured biomass values came from harvest or from the HTO method. It is concluded therefore that the HTO method is a reliable nondestructive means for biomass determination which is unbiased and which is suitable for whole forest biomass estimates. The biomass measurements require only little, easily obtainable extra data, over those needed for transpiration measurements.

The HTO technology for transpiration and biomass measurement has a high information yield for the effort invested. Most experimental forests are normally instrumented to acquire needed weather information and most forest research programs include measurements of plant population density and individual tree dimensions. The only additional data needed for a relatively complete description of forest hydrology is the results from a few HTO experiments with individual trees. Both the field and laboratory phases of the HTO experiments can be managed with few workers and results are obtainable over relatively short time spans after the completion of the experiments. More time is now consumed in the computational aspects of the experiments than in data gathering. In future experiments on forest hydrology with the HTO method it would be worth while to give some attention to the development of appropriate computer routines which could make the results available much more quickly than is now possible.

REFERENCES

ADDOR, E. E. 1972. Theodolite surveying for nondestructive biomass sampling. In: Research on coniferous forest ecosystems: A symposium. p. 167-176. Edited by J. F. Franklin, L. J. Dempster, and R. H. Waring. U.S. Forest Service Pub. 322 p.

BERGNER, P.-E.E. 1961. Tracer dynamics: I. A tentative approach and definition of fundamental concepts. J. Theor. Biol. 2: 120-140.

BERGNER, P.-E.E. 1964a. Tracer dynamics and the determination of pool sizes and turnover factors in metabolic systems. J. Theor. Biol. 6: 137-158.

BERGNER, P.-E.E. 1964. Kinetic theory: Some aspects on the study of metabolic processes. In "Dynamic clinical studies with radioisotopes." Ed. R. M. Kniseley and W. N. Tauxe. U.S. Atomic Energy Commission, Germantown, Md. p. 1-18.

BERGNER, P.-E.E. 1965. Exchangeable mass: Determination without assumption of isotopic equilibrium. Science 150: 1048-1050.

BERGNER, P.-E.E. 1966. Tracer theory: A review. Isotop. Radiat. Technol. 3: 245-262.

HINCKLEY, T. M. and D. R. SCOTT. 1971. Estimates of water loss and its relation to environmental parameters in Douglas-Fir seedlings. Ecology 52 (3): 520-524.

HINCKLEY, T. M. 1971. Estimate of water flow in Douglas-Fir seedlings. Ecology 52 (3): 520-525.

KLINE, J. R., J. R. MARTIN, C. F. JORDAN, and J. J. KORANDA. 1970. Measurement of transpiration in tropical trees using tritiated water. Ecology 5 (6): 1068-1073.

KLINE, J. R., C. F. JORDAN, and R. C. ROSE. 1971. Transpiration measurements in pines using tritiated water as a tracer. In "Proceedings 3rd Natl. Symposium on Radioecology." Oak Ridge, Tennessee, 10-12 May. In press.

KLINE, J. R., M. L. STEWART, C. F. JORDAN, and PATRICIA KOVAC. 1972a. Use of tritiated water for determination of plant transpiration and biomass under field conditions. In: Isotopes and Radiation in Soil-Plant Research Including Forestry." p. 419-437. Proceedings of IAEA Conference held in Vienna, Austria. Sponsored by IAEA and FAO. 674 p.

KLINE, J. R. M. L. STEWART and C. F. JORDAN. 1972b. Estimation of biomass and transpiration in coniferous forests using tritiated water. In: Research on Coniferous Forest Ecosystems - A Symposium. p. 159-166. Edited by J. F. Franklin, L. J. Dempster and R. H. Waring. U.S. Forest Service Pub. 322 p.

LJUNGGREN, K. 1967. A review of the use of radioisotope tracers for evaluating parameters pertaining to the flow of materials in plant and natural systems. Isotopes and Radiology Technology 5 (1): 3-24.

ORR, J. S. and F. C. GILLESPIE. 1968. Occupancy principle for radioactive tracers in steady state biological systems. Science 162: 138-139.

RANEY, F., and Y. VAADIA. 1965. Movements and distribution of HTO in tissue water and vapor transpired by shoots of Helianthus and Nicotiana. Pl. Physiol. 40: 383.

RITCHIE, GARY A. and T. M. HINCKLEY. 1971. Evidence of error in pressure-bomb estimates of stem xylem potentials. Ecology 52 (3): 534-536.

RUTTER, A. J. 1968. Water consumption by forests. In: Water Deficits and Plant Growth, Vol. II. T. T. Kozlowski editor. Academic Press, New York. 333 p.

SHIPLEY, R. A., and R. E. CLARK. 1971. Tracer Methods for In Vivo Kinetics. Academic Press, New York. 239 p.

STEWART, M. L., J. R. KLINE, and C. F. JORDAN. 1971. A tritiated water recovery system. Intern. J. Applied Rad. and Isotopes. 23: 387-388.

WARING, R. H., S. W. RUNNING, H. R. HOLBE, and J. R. KLINE. 1972. Modeling water uptake on coniferous forest Oregon watershed 10 synthesis. Coniferous Forest Biome Internal report 79. 20 p.

ZIERLER, K. L. 1964. Basic aspects of kinetic theory as applied to tracer distribution studies. In "Dynamic Clinical Studies with Radioisotopes." Ed. R. M. Kniseley and W. N. Tauxe. U.S. Atomic Energy Commission, Germantown, Md. p. 55-79

ZIMMERMAN, M. H. and C. L. BROWN. 1971. Trees Structure and Function. Springer-Verlag. New York. 336 p.

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 hours
$\bar{F}$	$cm^3\ hr^{-1}$	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 hours
$\bar{T}$	$cm\ sec^{-1}$	Transpiration rate given by solution of Montieth's equation which is averaged over the full experimental period
R_n	$cal\ cm^{-2} sec^{-1}$	Net solar radiation
S, S	$m\ bar\ ^{\circ}C^{-1}$	Change of saturation vapor pressure with temperature
ρ	$gm\ cm^{-3}$	Density of air
C	$cal\ gm^{-1}\ ^{\circ}C^{-1}$	Specific heat of air
λ	$cal\ cm^{-3}$	Latent heat of vaporization of water
Y	$m\ bar\ ^{\circ}C^{-1}$	Psychrometric constant
$e_s, \bar{e}_s$	m bar	Vapor pressure of water in the atmosphere at saturation; daily and extended averages
$e, \bar{e}$	m bar	Vapor pressure of water in the atmosphere; daily and extended averages
r_a	sec/cm	External forest resistance
$r_s, \bar{r}_s$	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

ΔR	cm	Thickness of sapwood
Cv	cm^3	Total water volume of tree
C	DPM cm^{-3}	Concentration of HTO in tree sap
T_m	hr	Mean residence time of water in a tree
D	gm	Biomass of water conducting parts of a tree
D_t	gm	Biomass of tree including heartwood
f		Fractional moisture content of tree on dry weight base
K		Ratio of heartwood to sapwood density
q	hr^{-1}	Fraction of total HTO which passes out of a tree per unit time
$w_i, \bar{w}$		Daily and extended averages of an unspecified weather variable which is proportional to transpiration rate

APPENDIX B.

Derivation of a means for obtaining the true mean value of transpiration in trees from the Stewart-Hamilton equation when auxiliary climatic data are available.

For any small increment of time the following material balance holds:

$$Mq\,dt = F_i C\,dt \tag{1}$$

Upon integration of both sides of (1) equation (2) is obtained since

$$\int_0^\infty q\,dt = 1.$$

$$M = \int_0^\infty F_i\, F(t)\; dt \tag{2}$$

If flow is constant in time then $F_i = F$, and F can be removed from inside the integral. This results in the Stewart-Hamilton equation. If F_i is not constant it cannot be removed from the integral. However, it is found experimentally that if F_i does not deviate too much from F during the course of the experiment the equation can be solved with small error and $F \simeq \bar{F}$.

When there are large deviations of daily flow (F_i) from mean flow ($\bar{F}$) equation (2) will not in general yield a correct solution for F. What follows is a derivation of a means for obtaining $\bar{F}$ under extremely varient flow conditions. This can only be accomplished if climatic data which are related to transpiration are available.

Suppose that for the full period of the HTO transpiration experiment there exists a climatic variable which is proportional to the transpiration rate as follows:

$$\bar{F} = K\bar{W}$$

$$F_i = KW_i$$

Then

$$\frac{F_i}{\bar{F}} = \frac{(W_i)}{\bar{W}}$$

and

$$F_i = \bar{F}\,\frac{(W_i)}{(\bar{W})}$$

Substitution for F_i in equation (2) yields:

$$M = \int_0^\infty \frac{\bar{F}}{\bar{W}}\quad (W_i)\; f(t)\,dt$$

but $\bar{F}/\bar{W}$ are constant for a given experiment so:

$$M = \bar{F}/\bar{W} \int_0^\infty (W_i)\ f\ (t)\ dt$$

True mean flow is therefore:

$$\frac{M \times \bar{W}}{\int_0^\infty (W_i)\ f\ (t)\ dt} = \bar{F} \tag{3}$$

Equation (3) has been solved using either Montieth's solution or net solar radiation as the weather variable. In most cases it was found to be unnecessary to use the solution since the value of F agreed well with $\bar{F}$ under a wide variety of conditions. In general this solution is not needed for conditions of variable cloudiness or short periods of rainfall during an experiment. The only case we have found where solution of equation (3) was needed was that of tree number 1 from the Cedar River Watershed.

In the experiment with tree 1 the full period of observation was 350 hours. The first 186 hours of this period after injection of HTO was characterized by solid overcast rainy conditions. This was followed by partly cloudy weather for the remainder of the experiment. Since climatic data were not available for this experiment equation (3) was solved by simply assigning a value of zero or one to the weather variables depending on whether or not transpiration was taking place. The value of zero was assigned to the weather variable for the first 186 hours of the experiment and one to all values thereafter. When this was done a flow rate of 1.45 ℓ/hr was obtained for the sunny protion of the experiment and 0.78 ℓ/hr for the average rate during the entire experiment. When the entire experimental activity-time curve was integrated without the correction a value of 1.0 ℓ/hr was obtained as the mean flow rate for the entire experimental period. In this extreme case the error in computed average transpiration was of the order of 30%. This indicates that even under severe interruptions of a transpiration experiment by rainfall the Stewart-Hamilton equation is quite stable and that in most cases it is not necessary to apply the correction.

APPENDIX C.

Daily values of weather variables and transpiration rates of the Oregon Tree

Day	Radia- tion	Temp	Satura- tion Deficit	Trans- piration (24 hr ave)	Trans- piration (Daylight)	Conduc- tivity (24 hr ave)	Conduc- tivity (Daylight)
	Ly/day	°C	m bar	1/hr	1/hr	cm/hr	cm/hr
1	672	18	7.01	12.9	22.1	3.2	5.5
2	660	21	10.44	17.6	30.1	4.4	7.5
3	690	19	9.22	15.8	27.1	3.9	6.7
4	708	18	7.84	14.1	24.2	3.5	6.0
5	684	17	8.13	14.0	24.0	3.5	6.0
6	372	12	3.64	6.1	10.4	1.5	2.6
7	216	11	2.89	4.3	7.4	1.1	1.9
8	456	13	3.29	6.3	10.7	1.6	2.7
9	480	15	3.75	7.2	12.4	1.8	3.1
10	666	22	11.89	19.6	33.6	4.9	8.3
11	654	24	15.21	23.9	41.0	5.9	10.2
12	660	24	14.62	23.3	39.9	5.8	9.9
13	636	22	11.10	18.4	31.5	4.6	7.6
14	648	23	13.48	21.5	36.9	5.4	9.2
15	642	25	21.53	31.3	53.6	7.8	13.3
16	594	27	23.88	34.2	58.6	8.5	14.6
17	582	27	20.68	30.4	52.1	7.6	13.0
18	582	26	17.14	26.0	44.6	6.5	11.1
19	606	20	8.88	15.0	25.8	3.7	6.4
20	636	20	7.95	14.2	24.4	3.5	6.1
21	552	13	3.89	7.5	12.8	1.9	3.2
22	666	17	8.72	14.5	24.9	3.6	6.2
23	600	19	10.54	16.6	28.5	4.1	7.1
24	528	23	12.64	19.4	33.3	4.8	8.3
25	594	25	17.10	25.8	44.2	6.4	11.0
26	546	25	15.20	23.1	39.6	5.7	9.9
27	576	25	15.20	23.4	40.1	5.8	10.0
28	588	27	18.18	27.6	47.3	6.9	11.8
29	576	28	21.17	31.2	53.5	7.8	13.3
30	582	29	23.23	34.0	58.3	8.5	14.5
31	624	23	15.73	23.9	40.9	5.9	10.2
32	624	23	16.12	24.0	41.1	6.0	10.2
33	444	19	11.20	16.2	27.7	4.0	6.9
34	318	21	13.42	18.0	30.9	4.5	7.7
Mean (N=25)	588	23	14.39	22.5	38.6	5.6	9.6

Table 1. Description of transpiration experiments performed at Cedar River and Andrews Experimental Forest.

Tree	Dbh (cm)	Number of injections	Volume per injection (ml)	Total volume (ml)	Specific activity (DPM/ml)*	Total activity (DPM)*	Date of injection
1CR	16.1	8	1	8	1.102E9	9.123E9**	19Jun-72
2CR	25.1	8	1	8	do	8.816E9	11Sep-72
3CR	16.9	8	1	8	do	do	do
4CR	30.7	9	1	9	do	9.918E9	do
5CR	10.7	4	1	4	do	4.408E9	do
6CR	18.9	8	1	8	do	8.816E9	do
7CR	33.8	8	1	8	do	8.818E9	do
8CR	13.8	4	1	3.5†	do	3.857E9	do
9CR	36.9	8	1	8	do	8.816E9	do
10CR	53.4	8	1	8	do	8.816E9	do
Oregon	76.2	20	1	20	4.655E9	9.919E10**	18Jun-72

*Values recorded in exponential notation; 1.102E9 = 1.102×10^9

**Activity corrected for syringe calibration

†Spill of 0.5 ml occurred during injection

Table 2. Transpiration rates measured in Douglas-fir on the Cedar River Watershed and the Andrews Experimental Forest.

	Without Rain					With Rain			
Tree	Amount of HTO (DPM)	Curve integral (DPM x hr) / ml	Flow rate (ℓ/hr)	Flow rate (ℓ/day)	Dates* (1972)	Curve integral (DPM x hr) / ml	Flow rate (ℓ/hr)	Flow rate (ℓ/day)	Dates** (1972)
1	9.12E9	6.28E6	1.45	34.8	27Jun-5Jul	11.7E6	0.78	18.7	19Jun-5Jul
2	8.82E9	5.11E6	1.73	41.4	11Sep-19Sep	6.63E6	1.33	31.9	11Sep-6 Oct
3	8.82E9	1.21E6	0.73	17.5	11Sep-19Sep	1.77E7	0.50	12.0	do
4	9.92E9	5.51E6	1.80	43.2	11Sep-19Sep	7.99E6	1.24	29.8	do
5	4.41E9	1.01E7	0.43	10.4	11Sep-19Sep	1.27E6	0.35	8.4	do
6	8.82E9	5.86E6	1.50	36.0	11Sep-19Sep	7.22E6	1.22	29.3	do
7	8.82E9				NA	7.62E6	1.15	27.8	do
8	3.86E9	7.14E6	0.54	13.0	11Sep-19Sep	8.04E6	0.48	11.5	do
9	8.82E9				NA	3.68E6	2.40	57.5	do
10	8.82E9	1.50E6	5.88	141	11Sep-19Sep	2.24E6	3.94	94.5	do
Oregon	9.92E10	4.48E6	22.1	530	18Jun-21Jul	NA	NA	NA	NA

*Dates after HTO injection when the weather was partly cloudy with negligible daytime rainfall. Transpiration values in this section are average rates (trees 2-10) for these weather conditions.

**Dates show interval required for complete loss of HTO pulse. Transpiration values (trees 2-10) are averages for all weather conditions in the indicated time interval. These conditions included partly cloudy weather initially followed by 6 days of solid overcast rainy weather starting 19 September and ending 25 September. This period was followed by partly cloudy weather again for the remainder of the HTO pulse.

Table 3. Effect of errors in net radiation and external resistance on transpiration computed by the ratio method using Montieth's equation for the Oregon Tree.

Variable	"True" value	Assumed value	"True" trans* (ℓ/hr)	Trans with* assumed value (ℓ/hr)
Net radiation (ly/hr)	30.1	421 ly/day	34.0	30.3
Net radiation	28.5	400 ly/day	7.5	10.8
External resistance (hr/cm)**	2.78E-5	2.78E-4	34.0	30.7
do	2.78E-5	2.78E-4	7.5	10.5
do	2.78E-5	2.78E-6	34.0	35.5
do	2.78E-5	2.78E-6	7.5	6.2

*Values are maximum and minimum transpiration which took place during the experimental period.

**"True" value from Rutter (1968) who gave a value of 0.1 sec/cm for external resistance. For a very tall forest the correct value may be closer to 0.01 sec/cm (2.778E-6 hr/cm). Error in external resistance however has minor effect on transpiration computed by the ratio method.

Table 4. Regression equations and computed statistics for transpiration relationships.

Relationship	Y variable	X variable	Equation	Coefficient of determination r^2	Computed F value	Remarks
1	Transpiration	Sapwood Cross Section	$Y = 0.206 + 0.00571X$	0.95	147.6	Cedar River
2*	Transpiration	Sapwood Cross Section	$Y = 0.272 + 0.00544X$	0.99	2746	Cedar River + Oregon
3	Leaf Biomass	Sapwood Cross Section	$Y = 6.19 + 0.0624X$	0.91	63.3	Cedar River
4*	Leaf Biomass	Sapwood Cross Section	$Y = 1.34 + 0.0846X$	0.99	1104	Cedar River + Oregon

*Correlations which include the Oregon data must be viewed with caution. Data from the Oregon experiment yield a single widely outlying point in each data set which tends to give unrealistically strong correlations.

Table 5. Mean transit time, apparent flow velocities and relative path lengths for water in an old-growth Douglas-fir of the Andrews Experimental Forest.

Height (meters)	Transit time (hours)	Apparent velocity (cm/hr)	Relative path length
20	265	8	1
30	260	12	0.6
40	263	16	0.5
50	267	20	0.4

Table 6. Needle - twig activity ratios observed during the HTO experiment with Douglas-fir in Oregon.

Date (1972)	Activity ratio (N/T)	Mean Daily temperature (°C)	Mean daily saturation deficit (mb)	Mean daily transpiration rate (ℓ/hr)
28 Jun	0.56	24	11.9	23.9
29 Jun	0.49	24	15.2	23.2
30 Jun	0.67	22	11.1	18.4
14 Jul	0.58	25	15.2	23.4
15 Jul	0.81	27	18.2	27.6
17 Jul	0.81	29	23.2	34.0
19 Jul	0.79	22	16.1	24.0
21 Jul	0.74	21	13.4	18.0

Table 7. Tree dimensions and wood density of experimental trees of the Cedar River watershed and the Andrews Experimental Forest.

Tree	Height (meters)	Inside dark Dbh (cm)	Sapwood thickness (cm)	Heartwood radius (cm)	Sapwood* density (gm/cm^3)	Heartwood* density (gm/cm^3)	Sapwood cross section (cm^2)
1	14.6	14.4	2.81	4.40	NM**	NM	102
2	18.7	23.0	3.94	7.56	0.379	0.370	236
3	15.2	15.2	2.39	5.20	0.421	0.399	96.0
4	18.0	27.9	3.70	10.2	NM	NM	280
5	11.0	9.6	2.47	2.33	NM	NM	55.3
6	18.3	16.7	3.10	5.23	0.516	0.512	132
7	17.0	30.8	4.20	11.2	NM	NM	390
8	14.6	12.0	2.26	3.72	0.459	0.440	68.9
9	27.1	33.2	4.26	12.3	0.502	0.470	387
10	24.8	47.9	7.53	16.4	0.392	0.416	954
Oregon	75.6	134	10.4	56.4	0.395	0.462	4020

*Data for trees 2 through 10 indicated no significant difference between heartwood and sapwood density. The value of $K = \phi_h/\rho_s = 1$ was used to solve equation (11). For the Oregon tree a value of $K = 0.462/0.395 = 1.17$ was used.

**NM = Not measured.

Table 8. Computed and measured dry biomasses for experimental trees of the Cedar River watershed and the Andrews Experimental Forest.

Tree no.	Flow (ℓ/hr)	Mean residence time (hr)	Sapwood biomass* (HTO) (kg)	Heartwood correction factor	Total biomass (HTO) (kg)	Total biomass (observed) (kg)	Leaf biomass (kg)
1	1.45	42	53.4	1.59	85.1	105	3.3
2	1.73	85	128	1.74	225	185	29
3	0.73	90	57.6	1.84	106	92.5	16
4	1.80	100	158	2.17	342	413**	
5	0.43	70	26.4	1.31	34.5	28.5	3.0
6	1.50	70	92.3	1.65	152	185	22
7	1.15	240	242	2.12	514	532**	
8	0.54	72	34.1	1.61	54.7	61.3	11
9	2.40	155	326	2.16	703	618	24
10	5.88	125	644	1.94	1250	1240	65
Oregon	22.1	266	5160	3.90	20100	16900†	350

*All values computed using moisture content of 114%. The confidence interval for moisture is 114% ± 1SE = 12%. The computed biomass values for the HTO method have corresponding uncertainities at least this large.

**Values estimated from relationship No. 4, Table 9, rather than direct harvest.

†Total biomass exclusive of bark as estimated by an alternate nondestructive field method. Estimated biomass with bark was 19000 kg.

Table 9. Regression equations and computed statistics for biomass relationships.

Relation	Y Variable	X Variable	Equation	Coefficient of Determination (r^2)	Computed F Value	Remarks
1	Computed Biomass	Observed Biomass	$Y = 5.96 + 1.02X$	0.99	949	Cedar River
2*	Computed Biomass	Observed Biomass	$Y = -112 + 1.19X$	0.99	7736	Cedar River + Oregon
3	Computed Biomass	R^2	$Y = -17.6 + 2.27X$	0.99	693	Cedar River
4	Observed Biomass	R^2	$Y = -18.6 + 2.202X$	0.99	784	Cedar River

*Correlations which include the Oregon data must be viewed with caution. Data from the Oregon experiment yield a single widely outlying point in each data set which tends to give unrealistically strong correlations.

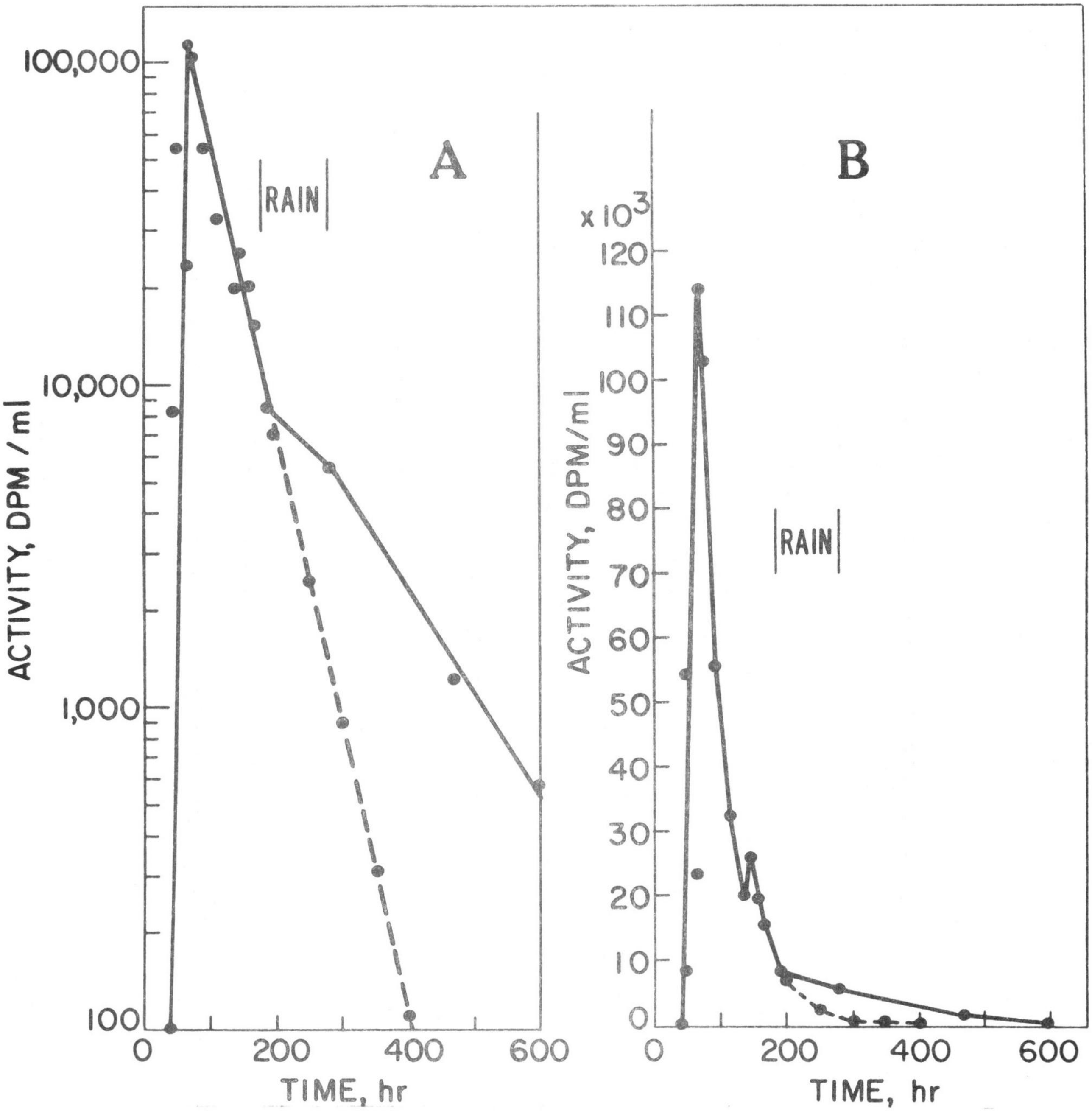

Figure 1. Activity-time curve for tree number 6 on the Cedar River Watershed plotted on semilogarithmic (A) and rectangular (B) coordinates. Steady rainfall which occurred during the interval shown changed the slope of the response curve. Dashed lines show the extrapolations which were made to obtain transpiration rates as if there had been no rain. The semi-log graph is used for the extrapolation and linear is integrated for transpiration.

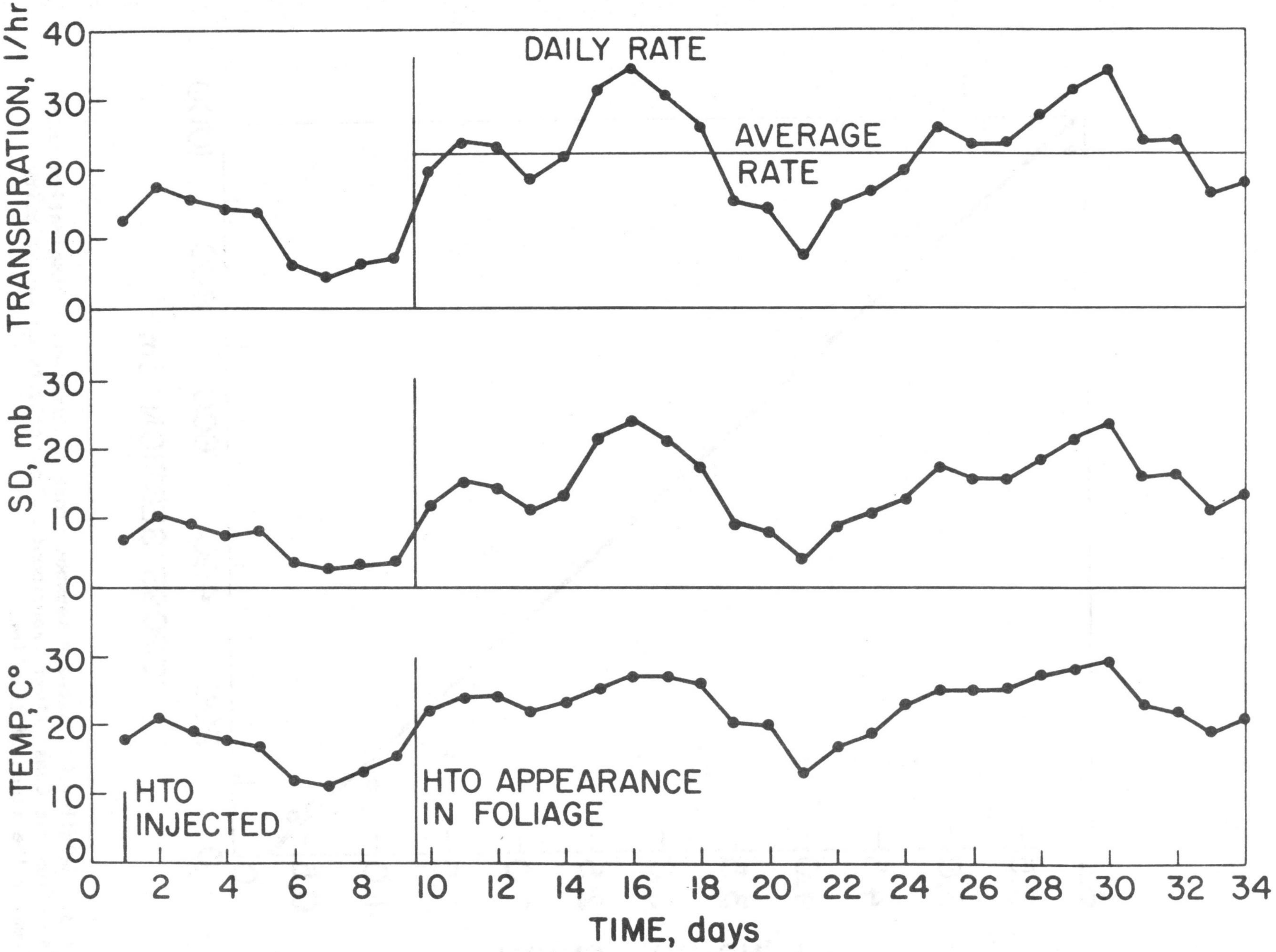

Figure 2. Daily average values of transpiration in the Oregon Tree (A), saturation deficit (B), and air temperature (C). The curve for daily transpiration rate has the same area under it as the one for average rate. Both curves account for the same total amount of evaporation water during the experimental period. The average rate from the HTO measurement starts from the time of first appearance of HTO in foliage.

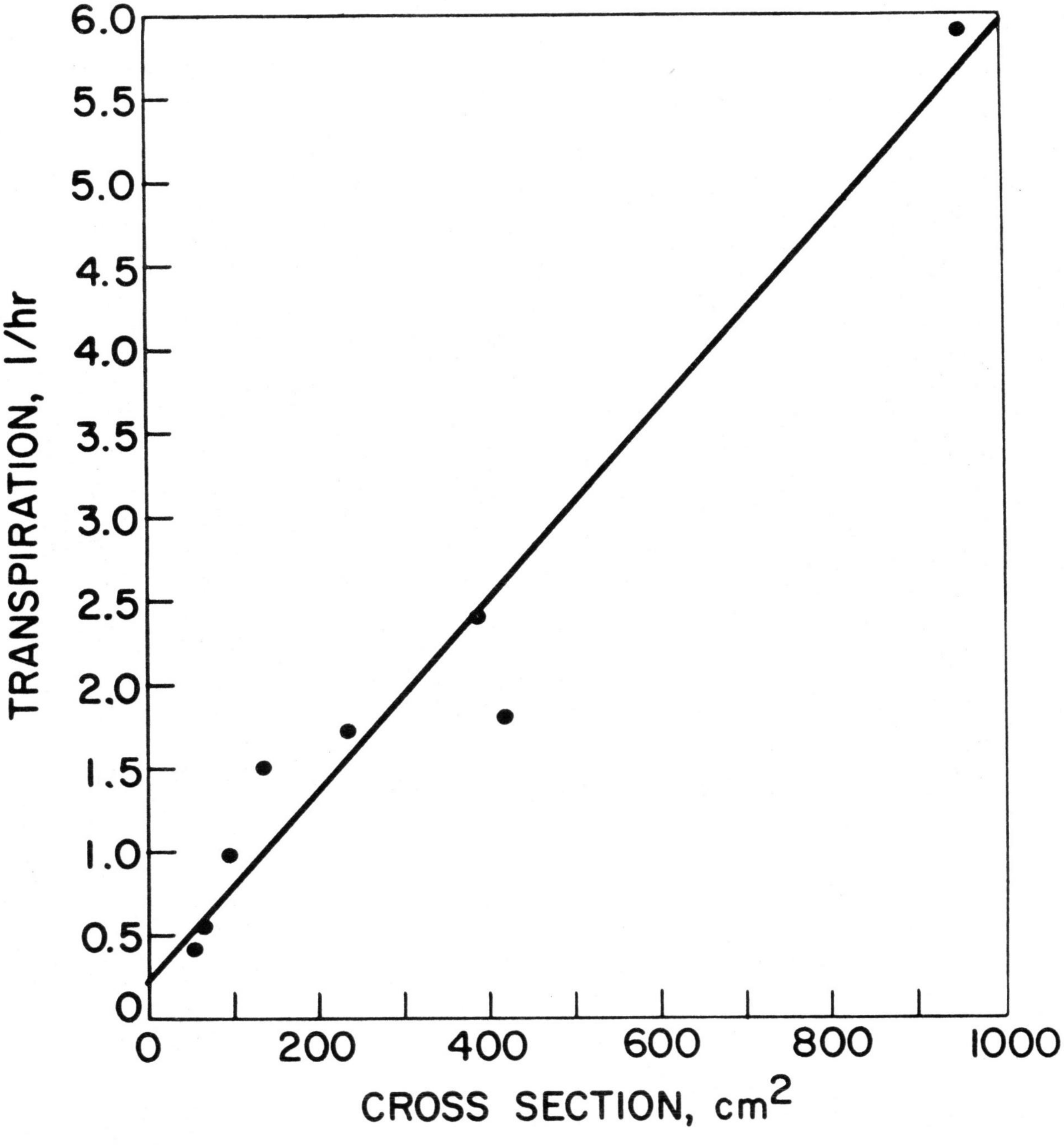

Figure 3. Relationship between sapwood cross section and transpiration rate in trees from the Cedar River experiment. Conductivity or sap velocity is given by the slope of the line.

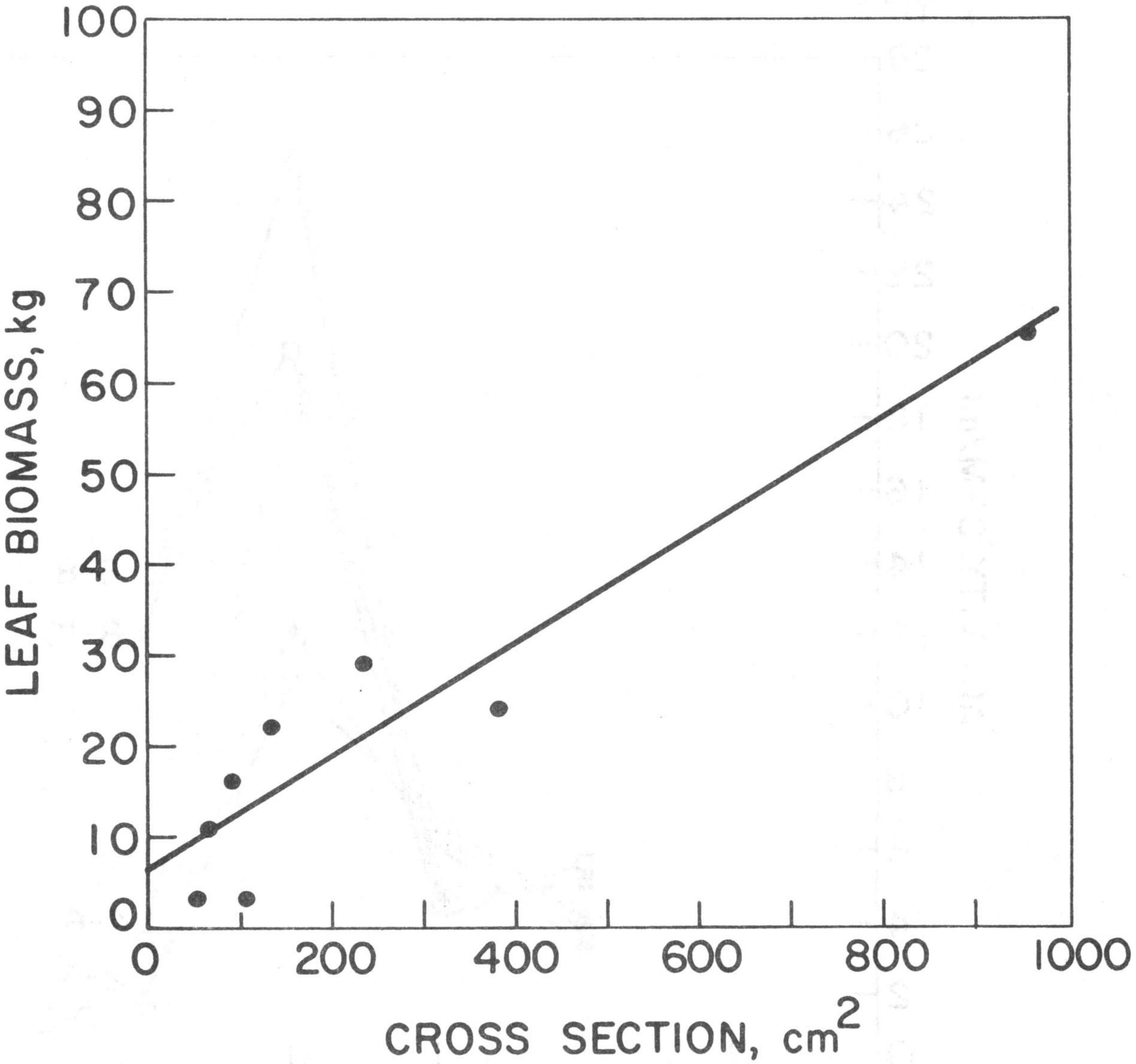

Figure 4. Relationship between leaf biomass and sapwood cross section in trees from the Cedar River experiment.

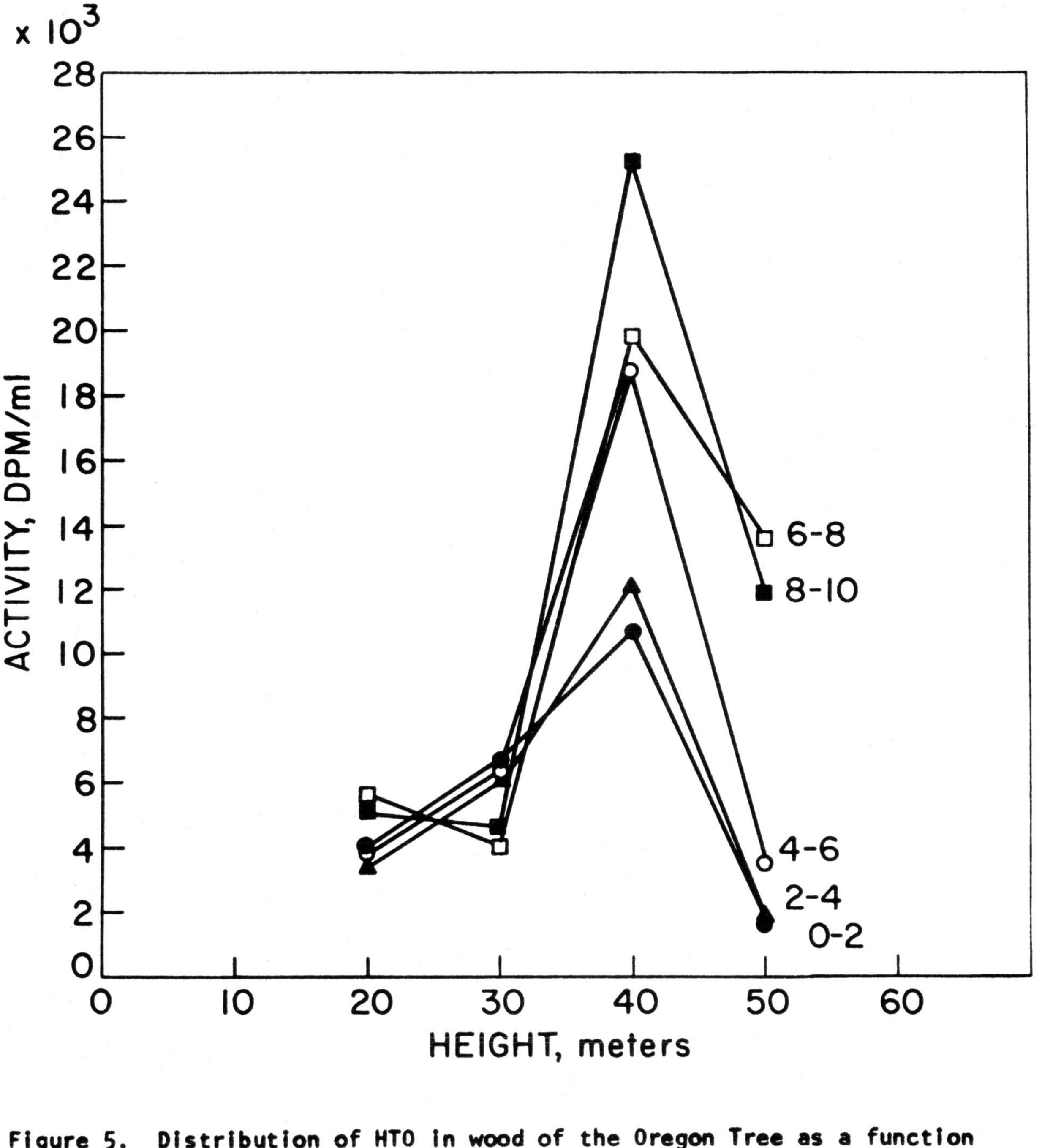

Figure 5. Distribution of HTO in wood of the Oregon Tree as a function of height. Numerical labels refer to depth of core in centimeters.

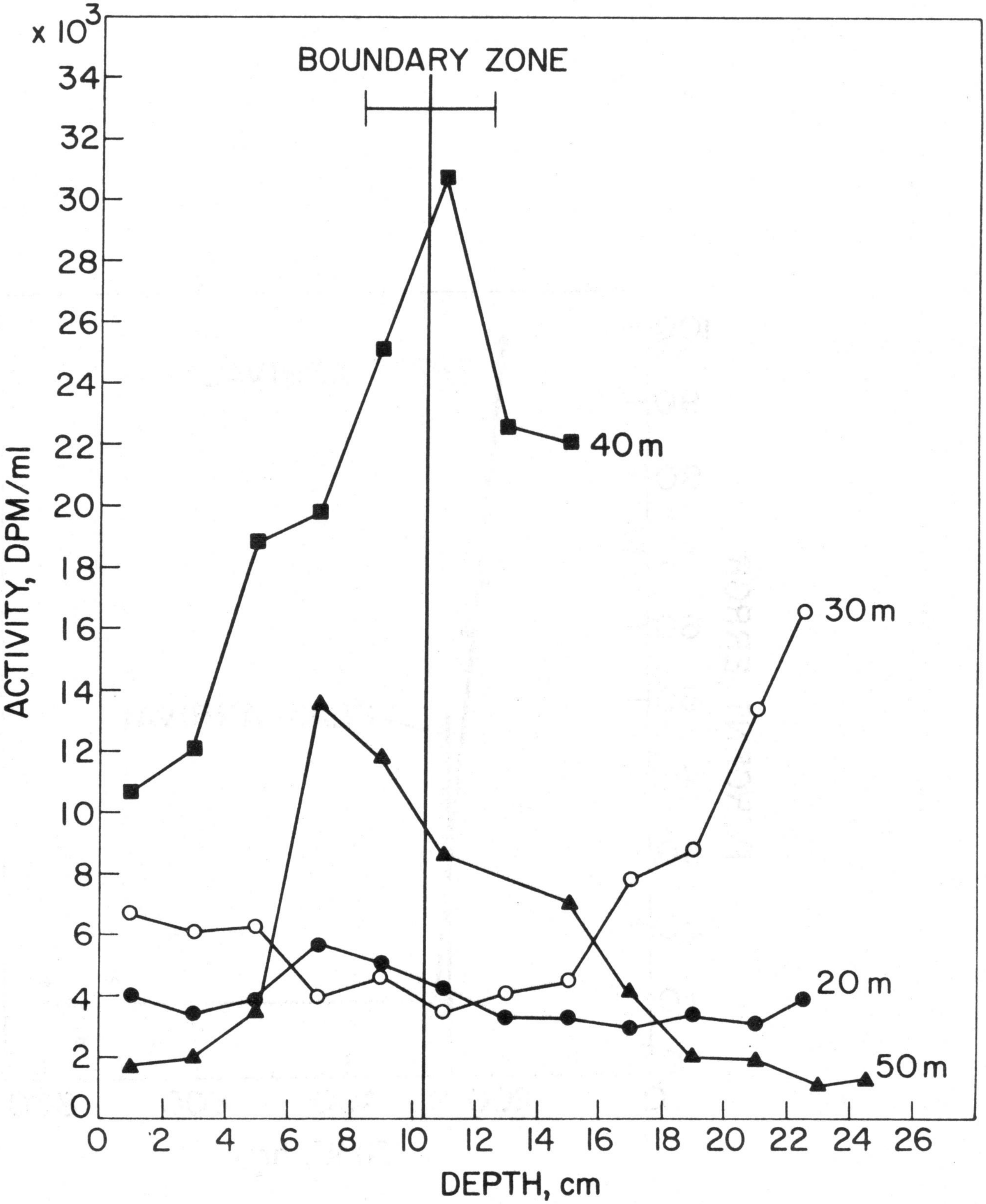

Figure 6. Distribution of HTO in the wood at various levels in the Oregon Tree as a function of depth. The boundary zone is the zone of separation between heartwood and sapwood. Error interval on the zone is 1 SE.

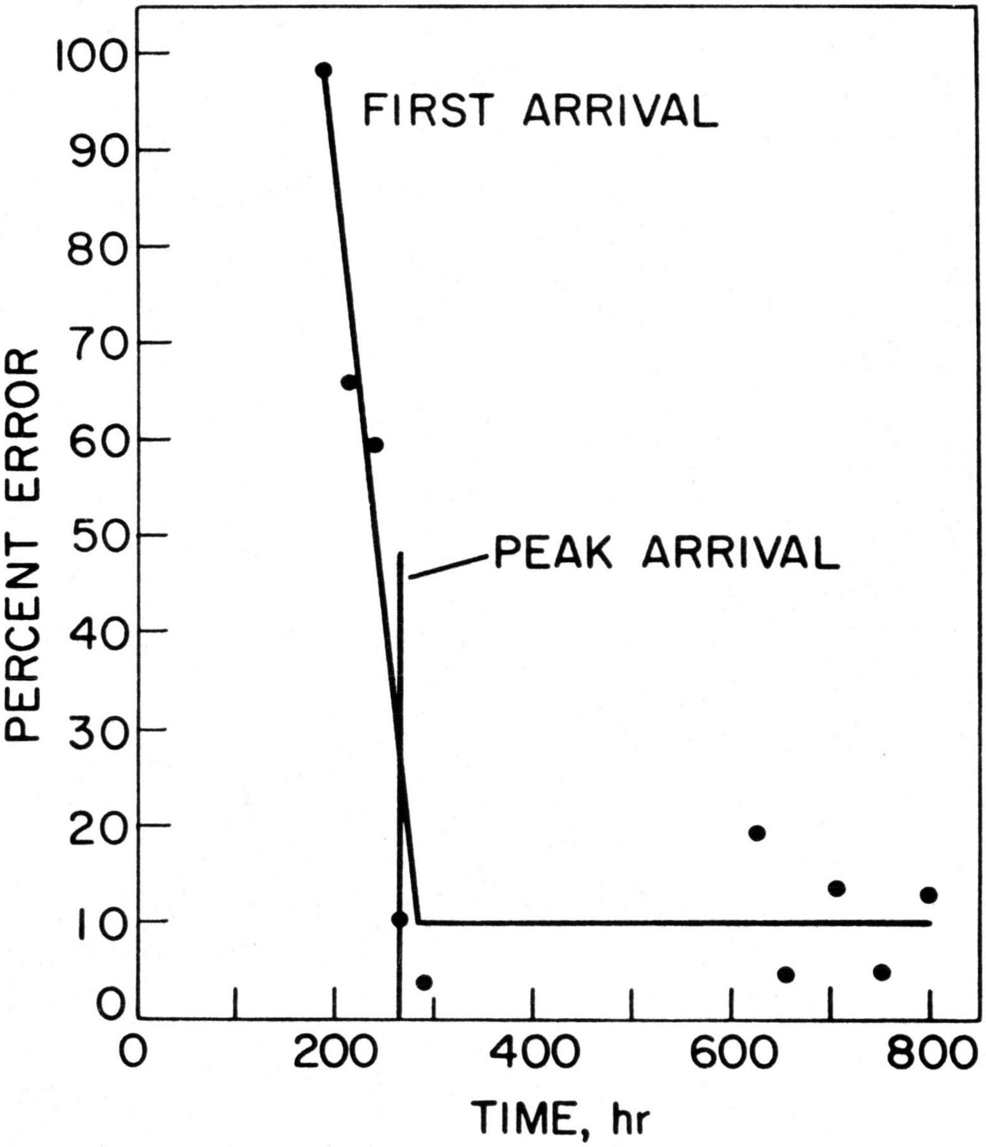

Figure 7. Change in percent standard error of HTO measurements in the Oregon Tree as a function of time. First arrival and peak arrival of HTO refer to the activity-time curve. Errors are at first very large but reach a minimum at about the time of peak arrival.

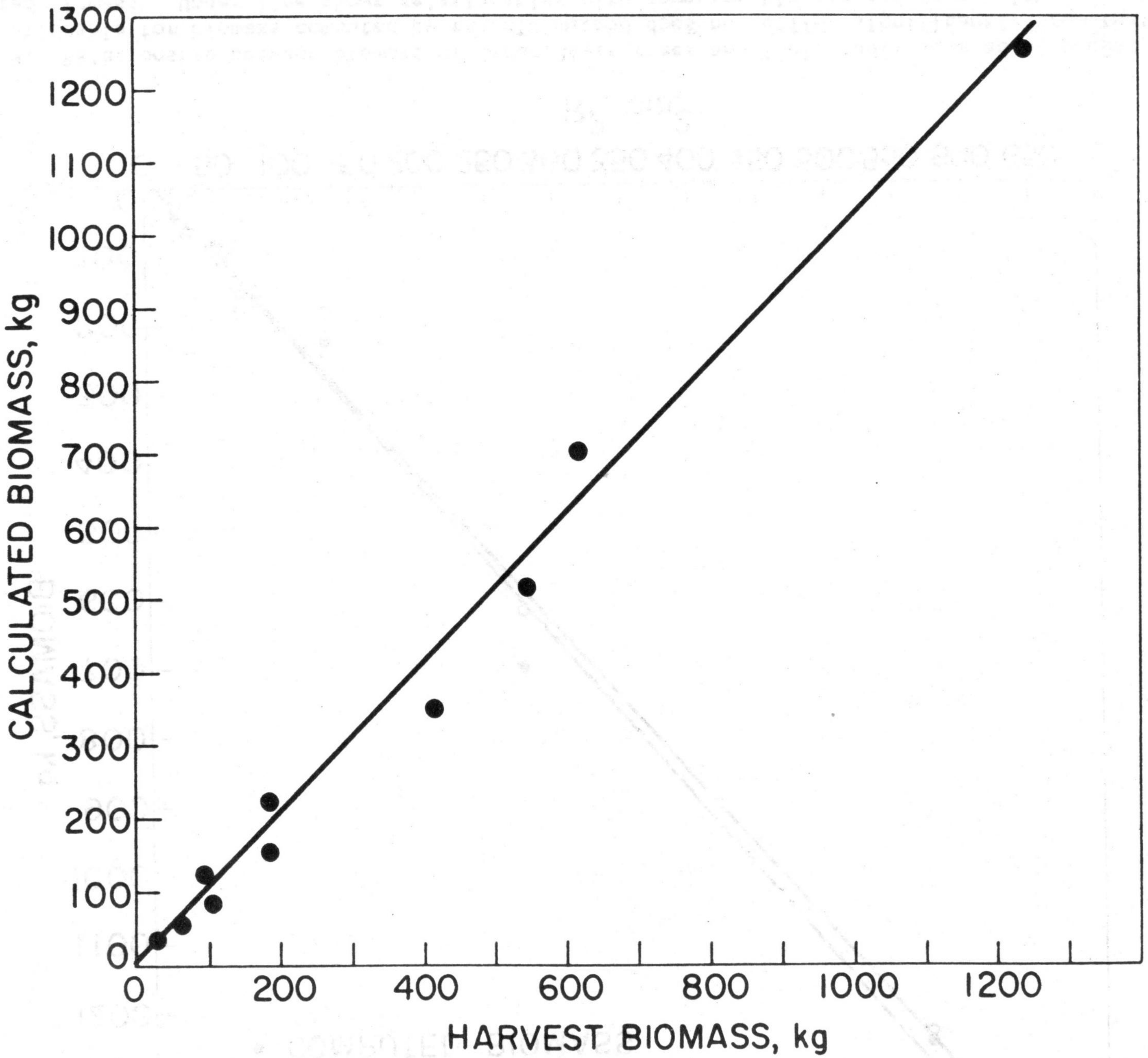

Figure 8. Relationship between biomasses of Cedar River trees as determined by the HTO method and by the harvest method.

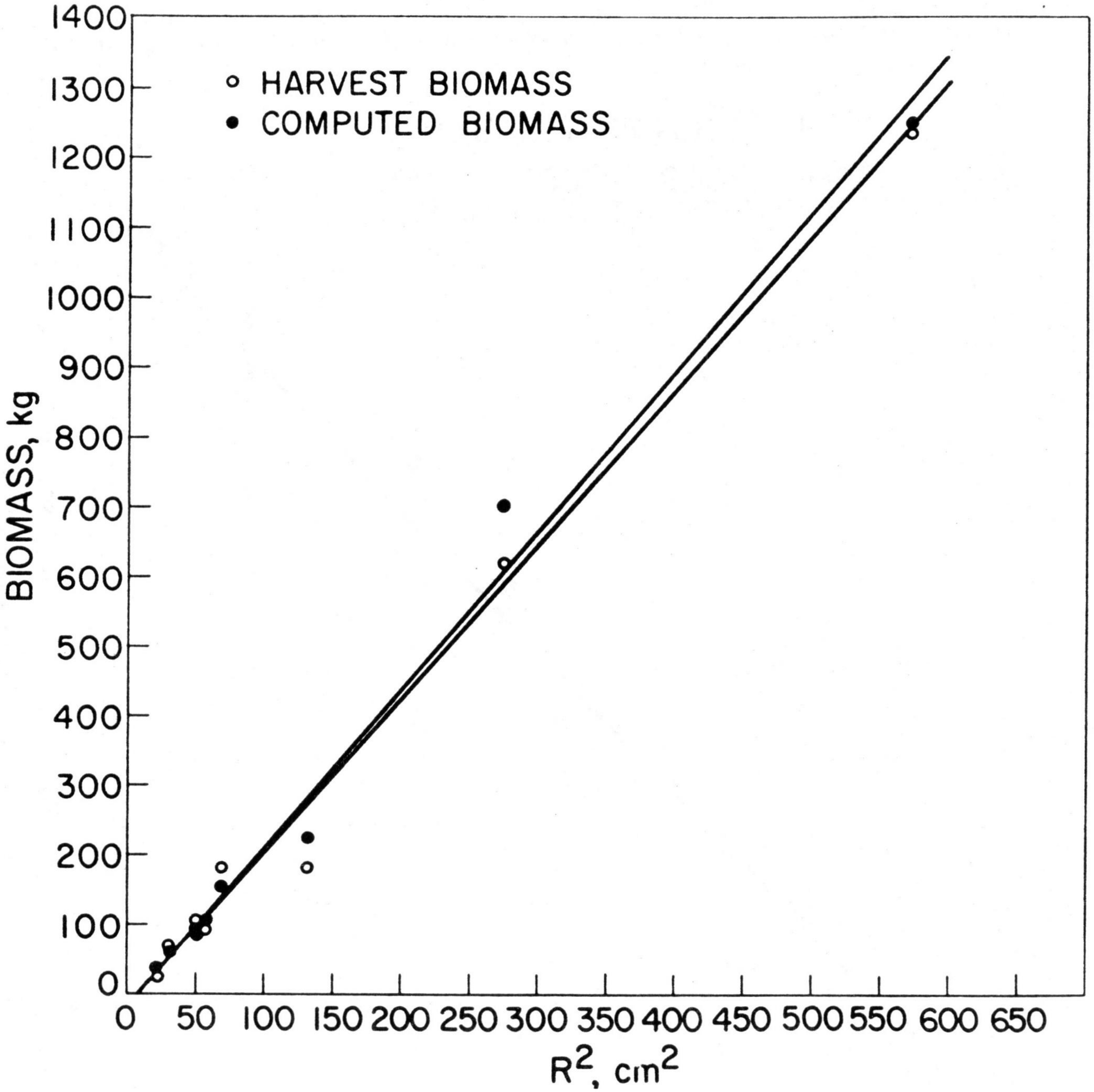

Figure 9. Relationship between biomass of Cedar River trees and their radii squared at breast height. The relationship for biomass computed by the HTO method does not differ significantly from that with the harvested biomass. Upper line shows relationships with computed biomass and lower with harvested biomass.