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MEASUREMENT OF SAP FLOW IN CONIFERS BY HEAT TRANSPORT [1]

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An account of the various methods which have been used in an attempt to measure the rate of sap flow in plants has been given by Crafts, Currier and Stocking (2). Methods which require the measurement of the amount of material moving through a known cross-sectional area, or the timing of the movement of some material indicator such as salts, dyes or radioactive material, suffer from the disadvantage that the vessels conveying the sap stream must be severed, either to measure the quantity of sap or to introduce the indicator, causing an unknown disturbance to the initial state. Our experience confirms that on cutting the vessels of a living tree the rate of sap flow always changes greatly in magnitude, often instantaneously.

Heat used as an indicator, however, does not have this disadvantage as it can enter the sap stream by thermal conduction through the walls of the vessels. Measurements using heat have been made by Huber (5) and his school (e.g., Huber and Schmidt (6)), and Dixon (3). Huber's first experiments were made on a tropical liana with such a high rate of sap flow that heat applied for one or two seconds was still recognizable as a pulse at the junctions of a thermocouple 30 cm downstream from the heater. The time till the first appearance of heat at the thermocouple was assumed to be the same as the time taken for the sap to move this distance.

For slower sap speeds it became essential to distinguish between the effect of convection by the moving sap and the transport of heat by thermal conduction. Dixon achieved this by placing the thermojunctions at distances of 1 cm and 2 cm from the heater and considering only cases when the more distant junction at some stage indicated a higher temperature than the nearer one. Huber and Schmidt (6) devised a method for the same purpose in which one junction was 2.0 cm downstream and the other 1.6 cm upstream from the heater. In all these experiments the heater wires and the thermojunctions were laid either on the intact bark or just under the bark on the surface of the sapwood.

There are two fundamental drawbacks to these heat transport experiments. First, it will be shown below that the assumption made in each case that the speed of the sap is identical with that of the heat pulse is not justified. In conifers the sap speed is actually about three times that of the heat pulse. Secondly, comparison between the curves presented for galvanometer deflections versus time and those calculated theoretically shows that, in spite of cotton wool lagging, there was considerable loss of heat; this reduces the usefulness of the results.

A detailed criticism of previous work is given below in the Discussion.

THEORETICAL

In order to avoid unknown surface losses, the present method uses a heater in the form of a straight line perpendicular to the surface, the temperature being measured at a point far enough below the surface to avoid the effect of these losses. The method of analysis adopted was the usual one of considering an idealized, simplified structure which is amenable to mathematical treatment, and then trying to explain discrepancies between the ideal, theoretical predictions and the experimental results by a reassessment of the simplifying assumptions involved in the mathematics.

For a start ignore the wood substance and consider the xylem to consist of nothing but sap, at rest in the first instance. Assume in these first illustrations that turbulence in the sap can be ignored. Consider a quantity of heat released instantaneously along a straight line in the sap. This heat will gradually diffuse throughout the sap by the process of heat conduction, until eventually all the sap has its temperature raised by the same infinitesimal amount (assuming the xylem to be effectively infinite in extent so that the surface effects can be ignored). The temperature at any point will rise to a maximum and then fall much more slowly to its original value (see fig 2). For a given quantity of heat the temperature at the point at a given time will depend only on the diffusivity of the sap, a quantity which depends on the thermal conductivity K, the density ρ, and the specific heat c of the sap. In fact

$$\text{Diffusivity, } k = K/\rho c.$$

Now consider the sap to be moving with uniform, parallel motion perpendicular to the straight line heater. In this case the movement of the pulse of heat will depend not only on conduction but also on convection due to the bodily movement of the sap.

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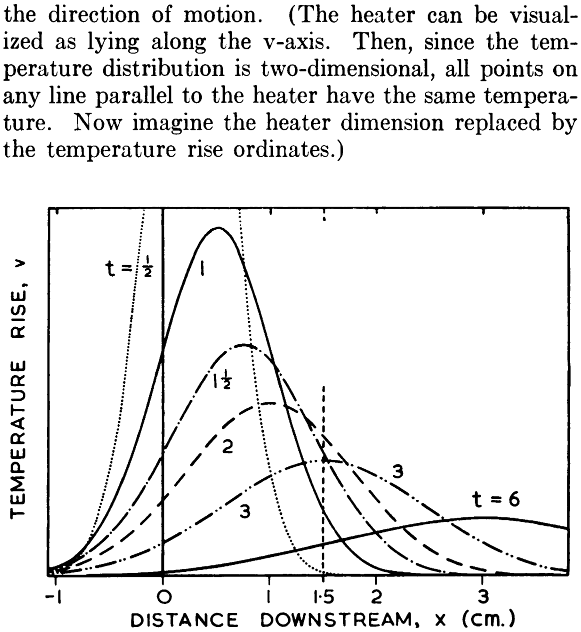
This is illustrated in figure 1, where the abscissa is the direction of motion. (The heater can be visualized as lying along the v-axis. Then, since the temperature distribution is two-dimensional, all points on any line parallel to the heater have the same temperature. Now imagine the heater dimension replaced by the temperature rise ordinates.)



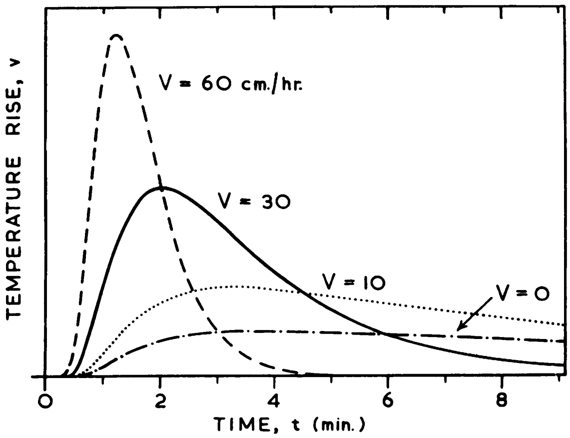


FIG. 1 (*top*). Theoretical temperature distribution at particular times, t (in minutes), after release of heat pulse. Heat-pulse velocity, V = 30 cm/hr. Diffusivity, k = 0.0025 cm^2/sec.

FIG. 2 (*bottom*). Theoretical curves of temperature rise against time at the point 1.5 cm downstream from the heater, for heat-pulse velocities, V = 0, 10, 30 and 60 cm/hr. Diffusivity, k = 0.0025 cm^2/sec.

As the heat pulse diffuses by conduction it is also moving with the steady velocity of 30 cm/hr. For instance, after three minutes the pulse is cylindrically symmetrical about the ordinate through x = 1.5 cm.

The temperature at a point directly downstream from the heater will rise to a greater maximum than if the sap were stationary, and at an earlier time. It will also return to its original value more quickly. Figure 2, for instance, shows curves of temperature rise against time from the release of the heat pulse, at the point 1.5 cm downstream in a medium with diffusivity, k = 0.0025 cm^2/sec for four different velocities, V cm/hr, of the medium. For a given quantity of heat, the temperature at a point at a given time will depend on both the diffusivity of the sap and its velocity. Figure 1 shows that when the effect of conduction is at all comparable with that of convection, the temperature rise at a point will reach its maximum value before the center of the heat pulse reaches the point. This is due to the rapid diffusion of the pulse. Consider, for instance, the situation at x = 1.5 cm; the temperature there is higher at 2 minutes than it is when the center of the pulse arrives at 3 minutes. Consequently the value obtained by dividing the distance to the point by the time to reach the maximum temperature will be an overestimate of the speed of the medium.

So far the xylem has been assumed to consist of nothing but sap. Consider a more realistic model, a material consisting of wood substance perforated by many uniformly spaced, parallel straight tubes through which sap flows at a uniform velocity. The way in which heat flows in this structure will depend on the time taken for any temperature difference between adjacent portions of sap and wood substance to disappear, and this in turn depends on the thickness of the tubes and the separating walls. Fortunately the xylem of a conifer like *Pinus radiata*, on which most of the present work has been performed, is sufficiently fine-structured to allow it to be treated as a homogeneous mixture from the point of view of heat transfer. The wall thickness of the tracheids is about 10 μ (8) and from the formula, $t = \frac{3l^2}{8k}$ (1, section 36) for the time t seconds required for a slab of thickness l cm and diffusivity k cm^2/sec to heat up to the temperature of its surfaces, we have $t \sim 10^{-4}$ seconds, taking the diffusivity of wood substance as 0.004 cm^2/sec. Since the time for the temperature to reach a maximum at the measuring point, 1.5 cm from the heater, is always of the order of minutes in practice, this time of 0.1 millisecond is quite negligible.

The case when the non-convecting material is so thick that the time to come to temperature equilibrium with its surroundings is not negligible, is complicated and has not been treated mathematically. This is discussed in the Results in the section on the Absence of Thermal Homogeneity.

The differential equation for conduction of heat in a homogeneous, isotropic solid with diffusivity k is:

$$\frac{\partial v}{\partial t} = k\left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} + \frac{\partial^2 v}{\partial z^2}\right) \qquad (1)$$

where v is the temperature.

If now a fraction, a, of any plane area perpendicular to the x-axis is occupied by sap streams moving with uniform velocity u parallel to the x-axis, then the layer of material bounded by the planes x and $x + \delta x$ gains heat at a rate per unit area equal to:

$$-au\rho_s c_s \frac{\partial v}{\partial x} \delta x$$

where ρ_s and c_s are the density and specific heat of sap. Inclusion of this term in the derivation of equation 1 yields the differential equation for combined conduction and convection:

$$k\nabla^2 v = \frac{\partial v}{\partial t} + au \frac{\rho_s c_s}{\rho c} \cdot \frac{\partial v}{\partial x} \qquad (2)$$

where k, K, ρ and c refer to the wet wood, i.e., the wood substance together with the stationary and the moving sap. For rising sap the positive direction of x (and u) is vertically upwards.

Dry wood is actually not isotropic, but has a greater conductivity along the grain (K_x) than across the grain (K_y and K_z). Wet wood may also be anisotropic although probably to a smaller extent. This can be allowed for (1, Section 13) by putting $y_1 = y\sqrt{K_x/K_y}$ and $z_1 = z\sqrt{K_x/K_z}$, which leaves equation 2 unaltered in form.

Equation 2 is of the same form as the equation for pure conduction in a medium moving in the x-direction with velocity:

$$V = au \frac{\rho_s c_s}{\rho c} \qquad (3)$$

(7); that is, the stationary wood and the moving sap together act like a single medium moving at a speed defined by V. This speed is less than that of the sap itself; it is in fact a weighted average of the velocities of the sap and the stationary wood substance. This is not altogether surprising when we consider that in the wood alone the heat pulse would remain stationary as it diffused, while in the sap alone the pulse would move at the same speed as the sap.

The solution for an instantaneous line source of heat along the z-axis, which is relevant to the present method, has been given for the case of a non-moving medium (1, Section 103):

$$v = \frac{Q}{4\pi kt} \exp\left[-\frac{x^2 + y^2}{4kt}\right]$$

(Q is defined to be the temperature to which the amount of heat liberated per unit length of the line would raise unit volume of the substance. This means, when c.g.s. units are used, that $Q\rho c$ cals/cm are released along the line.)

From this we can write the corresponding solution of equation 2:

$$v = \frac{Q}{4\pi kt} \exp\left[-\frac{(x - Vt)^2 + y^2}{4kt}\right] \qquad (4)$$

It will now be seen that figures 1 and 2 also apply to this model for green wood as well as to the case of xylem consisting of sap alone, and these figures were in fact calculated from equation 4. The diffusivity is now that of green wood, and may be expected to lie somewhere between the values 0.0014 and 0.004 cm^2/sec, the approximate values for sap (or water) and dry wood substance respectively. The diffusivity will not be known in any particular case since it depends on the moisture content of the sapwood and possibly on other factors.

Thus in general there are two unknown quantities which specify the nature of the heat flow, the diffusivity which is a measure of the heat conduction, and the heat-pulse velocity which measures the heat convection. The latter in turn must be related to the actual speed of the sap flow.

Even with considerable experience it is very difficult to make more than a rough guess at the diffusivity and the velocity associated with a temperature-rise versus time curve simply by visual inspection. Figure 4 gives some idea of the range of pairs of values for velocity and diffusivity which all give curves with the same time for maximum temperature rise at a given point, the sharper curves being associated with faster convection and lower diffusivity. The actual magnitude of the maximum temperature rise is different for each of these curves, but the temperature scale has been arbitrarily adjusted in each case to make all the curves pass through the same maximum point.

It is impractical to use the numerical value of the temperature rise for measuring purposes, owing to the difficulty of releasing an exactly known quantity of heat in the pulse, and of accurately calibrating the temperature measuring device. Instead formulae are used which enable the heat-pulse velocity and the diffusivity to be determined in terms of the relative temperature rises at known times. The most useful formula, which uses any three times such that the middle one is the average of the other two, will now be derived. Other formulae are derived in the appendix.

First eliminate Q, by substituting two points on the curve, (v_1, t_1) and (v_2, t_2), in equation 4 and dividing:

$$\ln\left(\frac{v_1 t_1}{v_2 t_2}\right) = -\frac{(x - Vt_1)^2 + y^2}{4kt_1} + \frac{(x - Vt_2)^2 + y^2}{4kt_2}$$

This may be simplified to give:

$$\ln\left(\frac{v_1 t_1}{v_2 t_2}\right) = \frac{(t_1 - t_2)}{4kt_1 t_2}(x^2 + y^2 - V^2 t_1 t_2) \qquad (5)$$

A similar equation may be written for points (v_3, t_3) and (v_4, t_4) giving a pair of simultaneous equations in k and V^2.

If the times t_1 to t_4 are chosen so that

$$t_2 - t_1 = t_4 - t_3 \text{ and } t_2 = t_3,$$

i.e., if

$$t_1 + t_4 = t_2 + t_3 = 2t_2,$$

the following solutions are obtained:

$$V = 60r\sqrt{\frac{t_1 \log_{10}\left(\frac{v_1t_1}{v_2t_2}\right) - t_4 \log_{10}\left(\frac{v_2t_2}{v_4t_4}\right)}{t_1t_2t_4 \log_{10}\left(\frac{v_1t_1v_4t_4}{v_2{}^2t_2{}^2}\right)}} \text{ cm/hr}$$

$$k = \frac{3.619r^2 (t_2 - t_1)^2 \times 10^{-3}}{-t_1t_2t_4 \log_{10}\left(\frac{v_1t_1v_4t_4}{v_2{}^2t_2{}^2}\right)} \text{ cm}^2\text{/sec} \quad (6)$$

where $r^2 = x^2 + y^2$ and t is in minutes.

More recently charts have been drawn which enable V and k to be read off directly from the ratios v_2/v_1 and v_4/v_1.

On carrying out experiments on actual trees a number of departures can be expected from the simplified model discussed here. In particular, it is known that as the sap flows through the xylem it follows devious paths from one tracheid to another, and so the assumption of parallel, uniform flow does not hold except as a first approximation. Again, the heater and temperature measuring probe are of finite dimensions and may cause distortions in the flow of the heat and of the sap. Then also, once the heat-pulse velocity has been found there remains the problem of obtaining a numerical value for the fraction a needed to relate this velocity to the actual speed of the sap flow.

Experimental Equipment

When making measurements on branches or roots under about 2 inches in diameter the simplest and best form of line heater is a length of 26 swg nichrome resistance wire threaded through a fine hole, usually along a diameter. A current of up to 40 amps is passed through this heater for 1 or 2 seconds by means of a 240/24V step-down transformer; the smaller the sap flow, the greater the current required for the same maximum temperature rise at a given point downstream.

For measurements in the sapwood of the trunk, both terminals of the heater must be at one end. The heater in this case consists of a piece of steel wire, which provides strength and a low electrical resistance, inside a tube woven of fiber glass. A piece of nichrome wire welded to the end of the steel returns outside the fiber glass and the whole assembly is bonded with a silicone varnish, the diameter being 2.5 mm. The whole length of the resistance wire must be well exposed on the surface, otherwise the heat-insulating effect of the electrical insulation causes a "tail" on the heat pulse which alters the shape of the temperature time curve to an unknown extent.

The temperature is measured by means of a Philips 83900 3K5 thermistor set in the tip of a 21 swg hypodermic needle, the needle itself forming one lead and the other passing up the hollow core. The thermistor forms one arm of a Wheatstone bridge which is supplied from an oscillator with 1 kc/s A.C. at about 1 volt. The out-of-balance signal is amplified, rectified and recorded on an Esterline-Angus recording milliammeter. The most sensitive range setting normally used gives a full scale deflection for about 0.5° F temperature rise and the heat input is usually chosen to give a maximum temperature rise of this order.

The thermistor probe and the heater are inserted in parallel holes drilled with the aid of a guiding block, the finer drills being simply chisel-ended pieces of blue steel wire. The spacing of 1.5 cm used most of the time is a compromise between the greater signal obtained with a smaller spacing and the associated increase in the percentage of error.

In field equipment under construction, the heating current will be supplied from an accumulator, and battery-powered electronic devices will operate indicating meters instead of a recorder.

Since iron is a much better conductor of heat than wood it might be expected that the probe would cause a local distortion in the temperature distribution in the wood by heat loss to the outside air. This possibility was examined by calibrating the thermistor at room temperature over a range of a few degrees, under three conditions; with the needle completely immersed in water, with 2.2 cm of the needle protruding into the water from the cork which is normally used to cover the exposed part of the needle, and with 1.0 cm of the needle protruding. Compared with the first case there was found to be a reduction in sensitivity of about 1.5 % in the second case, and 2.5 % in the third. Theoretical considerations indicate that a steady rate of heat loss through the needle, proportional to the temperature rise, is established within a few seconds, resulting merely in a slight reduction in the temperature rise scale of the curve, without distortion. This conclusion is supported by the fact that curves for zero sap flow, for which the effect of heat loss through the probe would be greatest (since the temperature rise stays at high values for a longer time), give an average value for the heat-pulse velocity of zero, although the effect of a considerable heat loss would be to increase the apparent value of this velocity because of the increased reduction of the temperature rise ordinate with time.

Experiments and Results

The experiments to test the validity and usefulness of the above theory fell into two stages. First it was necessary to find whether the curves of temperature rise versus time were in fact of the predicted type, after which it was necessary to find a practical way of deducing the rate of sap flow from the heat-pulse velocity.

Verification Experiments: The first experiments were made on pieces of cut-off branch which, having zero sap flow, eliminated one of the two unknown quantities, and thus facilitated comparison with theory. The experimental records obtained (fig 3 a) were analyzed by applying the formulae to numerous sets of three points on the curve. If each set gave zero for the heat-pulse velocity, and the

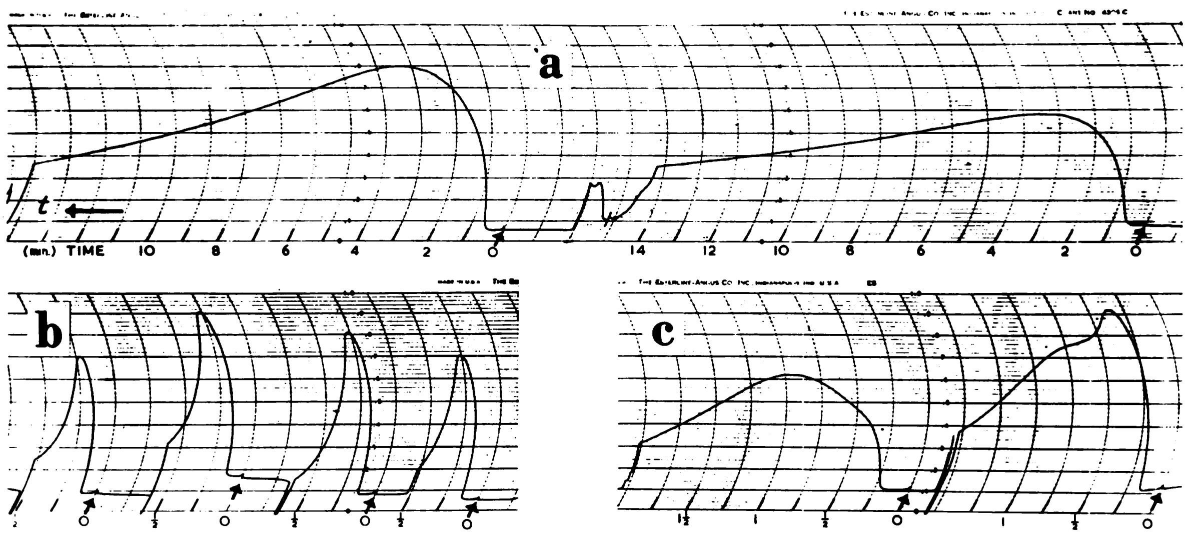


FIG. 3. Experimental records. The vertical arrows show the moment of application of heat. (The heater wire is left permanently in place while a series of measurements is made at one position.) Due to the construction of the recorder the ordinates (temperature) are circular arcs and the time axes (numbered in minutes) are reversed. The break-off at the tail of each curve marks the moment when the chart speed was switched to "slow" to await suitable conditions for another measurement.

(a) Analysis gives: Heat-pulse velocity, $V = 0$; diffusivity, $k = 0.0029$ cm^2/sec.

(b) For the right-hand curve analyses range from $V = 314$ cm/hr, $k = 0.00435$ cm^2/sec to $V = 283$ cm/hr, $k = 0.0102$ cm^2/sec. (For this measuring position when the flow was zero, $k = 0.0020$ cm^2/sec.)

(c) Double peaked curves. See text.

same value for the diffusivity this, of course, would indicate exact agreement with theory.

In fact, the values for the square of the heat-pulse velocity in cm/hr lie between $\pm$ 10, giving an average value very near the correct value (zero), and indicating a possible error for any one set of points of 3 or 4 cm/hr.

These and later experiments indicate that provided the thermistor is not less than about 0.5 to 1 cm below the surface, the finite dimensions of the piece of wood and the heater and probe do not cause any appreciable deviation from the theoretical case, with its assumption of an infinite medium and infinitesimal experimental apparatus.

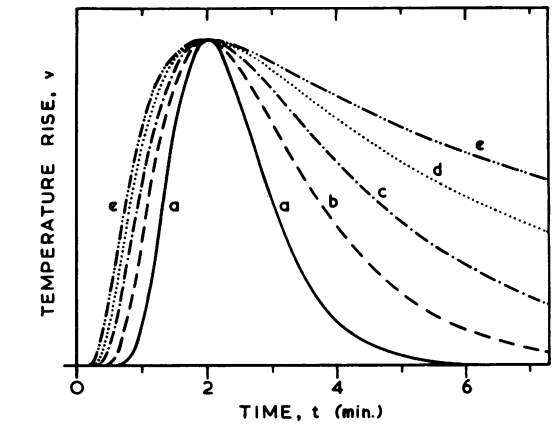
A complicating factor which appeared from the start is the variation of the ambient temperature inside the wood. This effect is always present to some extent and is inevitable when first making a measurement in a particular place because drilling the holes upsets the original temperature distribution. When the sap flow is comparatively fast the temperature settles down to a fairly steady value within a few minutes, and fortunately even in cases where the base line temperature continues to fall or rise for a long period it usually does so at a steady rate, which can be extrapolated with considerable accuracy for some minutes beyond the moment of application of heat. Uncertainty in this connection is probably the cause of the spread in the values calculated for the heat-pulse velocity above.

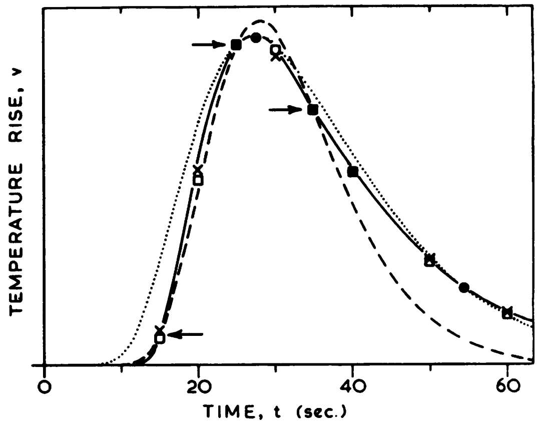
Experiments to test the case of non-zero sap flow were begun on a number of conveniently located conifers, mostly *Pinus radiata*, but the site of the experiments was soon transferred to a plantation of 12-year-old *Pinus radiata* on the sandhills at Woodhill, Auckland, New Zealand. Since it was permissible to mutilate these trees, we carried out dye experiments with acid fuchsin simultaneously with the heat experiments and were thus able to obtain some independent confirmation of the inferences from the heat experiments. The fact that dye experiments cause a major disturbance to the tree and the ultimate destruction of the part measured did not matter of course, in these exploratory experiments.

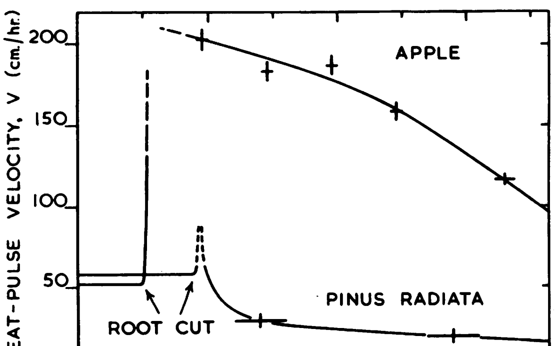
On analyzing the records obtained when the sap is in motion (e.g., fig 3 b) it is usually found that the calculated values for the heat-pulse velocity for particular sets of three points differ by up to 10 % between the greatest and the least, the value decreasing as the point corresponding to the longest time is taken further out on the tail of the temperature-rise versus time curve. (This time is usually not chosen greater than twice the time for the temperature to reach the maximum.) At the same time the calculated values for the diffusivity increase, but even the smallest value is usually considerably greater than the diffusivity measured at the same place when the sap flow is stopped, and this difference is greater the greater the heat-pulse velocity. (It is rather as if, for instance, the rising part of the curve were like that of curve b in fig 4 and the falling part like that of curve c in the same figure).

The explanation of these effects seems to be in the fact that the various sap streams whose combined effect produces the recorded curve are flowing at different speeds. If instead of assuming one uniform speed for the sap, it is assumed that all speeds within a certain range are present with equal effect, it has been found possible in the two or three cases tried, to find a theoretical curve which fits the experimental one almost exactly. This is illustrated in figure 5, where the full line is the experimental curve. Analysis of the three points marked with arrows gives 178 cm/hr for the heat-pulse velocity and 0.0031 cm^2/sec for the diffusivity. The correct curve for these values is shown by the pecked curve (which intersects the experimental curve at the three analysis points). Similarly analysis of the two points indicated by a solid circle gives heat-pulse velocity 168 cm/hr and diffusivity 0.0059 cm^2/sec, the correct curve for these values being shown dotted. Neither of these calculated curves fits the experimental curve at all well, but if a uniform distribution of heat-pulse velocities between 97 and 240 cm/hr is assumed, with a diffusivity of 0.0025 cm^2/sec for the green wood, the 8 points marked by crosses are obtained. The points marked by hollow squares, which fit the experimental curve a little better than the crosses at some points and not quite so well at others, correspond to a spectrum between 100 and 238 cm/hr with a diffusivity of 0.0023 cm^2/sec.

Notice that the diffusivity associated with the spectrum of velocities is between 0.002 and 0.003 cm^2/sec, approximately the same as the values ob-







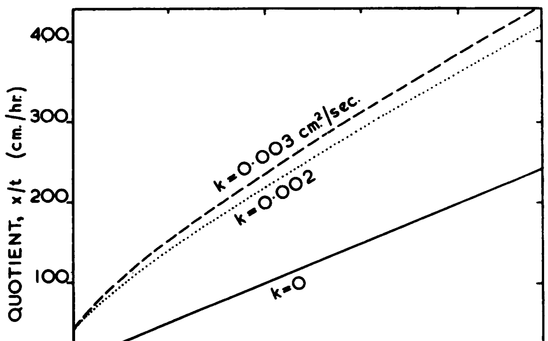


FIG. 4 (*top left*). Theoretical curves for various heat-pulse velocities, V, and diffusivities, k, at 1.5 cm downstream. (a) V = 39.9 cm/hr. k = 0.001 cm^2/sec. (b) V = 34.1 cm/hr. k = 0.002 cm^2/sec. (c) V = 27.0 cm/hr. k = 0.003 cm^2/sec. (d) V = 17.2 cm/hr. k = 0.004 cm^2/sec. (e) V = 0. k = 0.00469 cm^2/sec.

FIG. 5 (*top right*). For explanation see text.

FIG. 6 (*bottom left*). The change in sap speed on cutting roots.

FIG. 7 (*bottom right*). Theoretical curves for the quotient x/t = distance/time to "first onset" at the point 2 cm downstream against heat-pulse velocity, V, for the cases of diffusivity, k = 0.002 and 0.003 cm^2/sec. (Q and v in equation 9 were chosen to make both curves go through x/t = 40 cm/hr at V = 0.) The full line is the curve that would be obtained if there were no conduction, only convection, i.e., if V = x/t.

tained in the absence of flow. The over-simplified analysis assuming a single velocity, attributes the spreading out of the heat pulse to a high diffusivity.

The mathematical expression for the temperature rise in the case where there is a uniform distribution of heat-pulse velocities between V_1 and V_2 is obtained by integrating equation 4:

$$v = \frac{Q}{4\pi kt} \times \frac{1}{V_2 - V_1} \int_{V_1}^{V_2} \exp\left[- \frac{(x - Vt)^2}{4kt} \right] dV$$

$$= \frac{Q}{4t\sqrt{\pi kt}\,(V_2 - V_1)} \left[\mathrm{erf}\left(\frac{x - V_1 t}{2\sqrt{kt}}\right) - \mathrm{erf}\left(\frac{x - V_2 t}{2\sqrt{kt}}\right) \right]$$

where erf is the error function defined by (1, Section 20):

$$\mathrm{erf}\, w = \frac{2}{\sqrt{\pi}} \int_0^w e^{-x^2} dx$$

Variations in the rate at which the sap flows through the xylem are to be expected, since the sap as it flows from one tracheid to another may encounter varying degrees of resistance. On a larger scale, dye experiments show that the flow rate may differ greatly between paths separated laterally by a few mm.

Some caution must be exercised, however, in applying this explanation in all cases, for measurements described below in the section on the Absence of Thermal Homogeneity show that a similar apparent spread in speed values can be caused by regions of non-convecting material more than a few mm thick, for which the assumption of thermal homogeneity essential to the mathematical analysis breaks down.

Since the appropriate values for the limits of the spectrum of heat-pulse velocities for a particular recorded curve can only be found by laborious trial and error, the records in practice have been analyzed as if the velocity were single valued. In the cases treated in detail the values obtained were close to the average value for the spectrum (as may be verified in the case of fig 5). These findings on the non-uniformity of the sap flow, however, necessitate a reassessment of whether the "sap speed" is the most useful concept for describing the rate of sap flow. This matter will be discussed below.

Calibration Experiments: The general validity of the theoretical analysis having been established, there remained the problem of relating the heat-pulse velocity to the rate of sap flow. Equation 3 cannot be applied directly because the fraction a is not known; it cannot be deduced from the moisture content of the xylem because only a portion of this moisture consists of moving sap.

During the simultaneous dye and heat experiments discussed above some attempt was made to obtain a direct calibration of the heat transport method against the distance moved by the dye in a known time. Although this procedure would make the present method simply a refinement of the dye method it would still have the great advantage that once a calibration had been obtained for a particular tree, further measurements could be made on the same part of similar trees without disturbing them beyond drilling holes for the heater and probe. There is still the disadvantage, however, that it is not known whether the dye travels as far as the sap before being deposited on the vessel walls, and in any case the dye will only indicate the maximum speed along a given dyed path without giving any indication of the variation in speed in that path.

In actual fact the wide variation over the cross-section in the distance travelled by the dye allowed only a rough estimate of the average sap speed, but it was usually between two and four times the heat-pulse velocity. (This corresponds to a value for the fraction a of the right order, somewhere between 15 and 40 %.) Although this aspect of the experiments was not very useful, some of the results obtained are instructive in showing the kinds of change in the sap flow that may occur when the sap vessels are cut. Two cases are illustrated in figure 6. Both measurements were made on roots, about a foot away from the trunk. A length of split rubber tube was clamped at each end around the root and filled with dyed water, and then the root was cut under the water at a point about one foot below the measuring position.

The case of *Pinus radiata* is typical. After a momentary increase (shown by dye measurements), the flow decreases steadily. The case of apple was the only measurement made on a hardwood. Drought conditions were prevailing and the consequent sap tension, and the removal of the flow resistance at the roots probably explain the fourfold increase in sap speed. It should be noted that this graph shows only relative changes in the sap speed since the ordinate is the heat-pulse velocity.

(The length of the arms of each cross in fig 6 is a rough measure of the uncertainty in the velocity measurements, or the time to take the measurement. The unexpectedly fast flow in the apple root prevented the use of the most suitable recorder chart speed. Note that the faster the flow, the shorter the time for each measurement and the more rapidly they may be repeated.)

Since the experiments at this stage showed, 1st that the sap speed may be far from uniform, and 2nd that some of the analytical precision of the heat transport method of measurement would be lost in attempts at purely empirical calibration, it was questioned whether the sap speed (necessarily an average value) was the best measure of the rate of sap flow. The alternative was to use the volume rate of flow, i.e., the number of cc of sap crossing each sq cm of sapwood perpendicular to the direction of flow in unit time. This concept is well known to physicists as "flux."

It appears that values for sap speeds may be used for two purposes, either to compare rates of sap flow at different times and different places (in the same tree or different trees), or to relate the sap flow to other numerical quantities such as the rate of evaporation from the leaves, or the moisture intake at the roots. For the first purpose the sap flux is just as useful a measure as the sap speed, and for the second it is more useful because, to relate the sap speed to quantities like the above (evaporation, moisture intake), the speed must first be multiplied by the unknown factor a. For these reasons, and because the relation between the heat-pulse velocity and the sap flux is easily expressed in terms of quantities familiar to the timber technologist, it was decided to use the sap flux as the measure of the sap flow.

The quantity a u in equation 3 is, in fact, the sap flux, and so the equation may be written:

$$\text{Sap flux} = au = \frac{\rho c}{\rho_s c_s} V \quad (7)$$

The coefficient of V can be expressed in terms of the basic density and the moisture content of the sapwood:

$$\text{Basic density} = \rho_b = \frac{\text{oven dried weight of wood}}{\text{green volume}}$$

$$\text{Moisture content} = m_c = \frac{\text{green weight} - \text{oven dried weight}}{\text{oven dried weight}}$$

It is evident that ρ, the density of the green wood, is given by:

$$\rho = \rho_b(1 + m_c)$$

The specific heat is given by:

$$c = \frac{c_w + m_c c_s}{1 + m_c}$$

where

c_w = specific heat of oven-dry wood = 0.33 (4)
c_s = specific heat of sap (water) = 1.00
ρ_s = density of sap = 1.0

On substitution, equation 7 becomes:

$$\text{Sap flux} = \rho_b (m_c + 0.33)V \quad (8)$$

The moisture content is to be expressed as a decimal fraction (not a percentage) and the density in g/cc. Then if the heat-pulse velocity, V, is in cm/hr the flux is in cc/sq cm/hr.

The verification of equation 8 was carried out in laboratory experiments in which water was sucked through a length of wood by means of a vacuum pump. Roots or slender tree tops were discarded after a brief trial because even with the end surfaces freshly cut the flow decreased too rapidly with time, and varied too much over the cross-section.

With the object of getting a more uniform rate of flow over the cross-section, dowels 2.8 cm in diameter were made from the sapwood of freshly milled pine timber and lacquered on the sides to prevent air leak. Each cross-section contained parts of three annual rings which were about 1 cm wide. These dowels were found to have the added advantage that the flow rate decreased only very slowly with time, allowing greater control over the experiments.

The flux was measured by dividing q, the volume rate of flow of water through the dowel (in cc/hr) by the area of the convecting cross-section (in sq cm). The dye—in these experiments basic fuchsin decolorized with sodium metabisulphite—now served simply to define this convecting area.

Very dilute dye was run continuously while simultaneous measurements of the volume flow rate, q, and the heat-pulse velocity, V, were made with different rates of flow. These two measurements, q, and V, were found to be closely proportional, confirming that the heat-pulse velocity is indeed a measure of the rate of sap flow.

In verifying equation 8 the uniformity of flow over the cross-section was first checked by taking a series of heat-pulse velocity measurements with the tip of the thermistor probe at intervals of about 3 mm along a diameter of the dowel. (These measurements were useful only when the depth was greater than about 5 mm since the effect of heat loss at the surface becomes noticeable at shallower depths.) On the occasion when the uniformity was carefully checked in this way, the cross-section was found to be completely dyed except for two strips 1 or 2 mm wide at the late wood. In this case and in others where the dye pattern was similar, the formula of equation 8 was found to be true within the experimental error (a few percent). It does not seem worthwhile to quote the numerical values here since in these laboratory experiments the rates of flow were about four times greater than the highest measured in a living tree (the latter being about 90 cc/sq cm/hr).

ABSENCE OF THERMAL HOMOGENEITY: When there are bands of non-convecting material wide enough to cause the condition of thermal homogeneity to break down, the results are not so easily interpreted. This situation has not been treated mathematically but a qualitative picture can be obtained from simple reasoning. Consider a non-convecting region abutting on to the thermally homogeneous region at a plane parallel to the direction of sap flow, and consider a cylindrical pulse of heat perpendicular to the boundary. As this pulse moves forward with the heat-pulse velocity of the convecting region, the effect of the non-convecting region is to retard the pulse near the boundary, while at the same time the pulse extends with further retardation into the non-convecting region. For, as the pulse moves forward due to convection, heat will be transferred by conduction from the forward part into the non-convecting region, while at the trailing edge of the pulse some of the heat deposited previously will be conducted back into the convecting region.

These considerations are supported by experiments on a dowel which contained both sapwood and heartwood running parallel to the length of the dowel. The zero flow in the heartwood was shown by complete absence of dye. Measurements made with the thermistor at various points along a diameter perpendicular to the boundary of the two regions gave non-zero values for the heat-pulse velocity at depths up to 7 mm into the heartwood, the values decreasing approximately linearly with depth. Analysis based on the assumption of a spectrum of velocities indicated a wide spectrum with values ranging down to zero.

It is possible that the uniform speed analyses of this case may be taken at their face value, on the interpretation that the heat transport method measures the sap flux over an area about 2 cm across centered on the thermistor (when this is spaced 1.5 cm from the heater), and that there is still some flux across this area as long as the thermistor is less than about 1 cm into the heartwood.

In the same dowel there was a non-convecting band about 5 mm wide flanked by dyed regions. Here curves were obtained with two peaks corresponding to heat-pulse velocities of about 225 cm/hr and 65 cm/hr, the relative magnitudes of the peaks changing when the thermistor was moved. It would appear that the water in the neighboring regions was moving with quite different velocities—certainly this is further evidence that a moving pulse extends beyond the actual region of flow (fig 3 c).

Discussion

It is clear that the findings described in this paper necessitate a reinterpretation of all previous sap flow measurements made by heat transport methods. Previous workers have limited themselves to finding the heat-pulse velocity, assuming this to be the same as the sap speed, and have not always been successful even in obtaining this velocity. Huber appears to be the only one to attempt calibration experiments (6) when he compared the results of his "compensation method" with the rate of flow of water through twigs, measured in drops per second. At best such experiments could show no more than a proportionality between the heat flow measurements and the volume rate of sap flow; there is no question of an absolute comparison with sap speed. Huber simply assigned to a particular flow rate (in drops/sec) the speed indicated by his earlier heat transport method, which itself was based on the assumption that the time to the first appearance of a temperature rise at the nearest thermojunction to the heater was the time for the sap to travel the distance between heater and junction.

Since the methods used by Huber and his school (the originators and principal users of heat transport methods) are based on this concept of the "first onset" of heat, it is instructive to consider the theoretical connection between the heat-pulse velocity and the time of first onset; that is, the time, t secs for the temperature at a point distant x cm directly downstream from the heater to rise by a certain amount, v° C. This is easily obtained from equation 4. Admittedly this equation applies to the case of homogeneous thermal mixing and absence of external heat loss, whereas most of Huber's experiments were performed on hardwoods with comparatively large sap vessels and with measuring devices just under the bark. But it is almost certain that the appropriate equation for all cases of convective heat diffusion will include the exponential term in equation 4, which is the most important term in the present connection. One finds that:

$$V = \frac{x}{t} - \sqrt{\frac{4\alpha k}{t}} \qquad (9)$$

where

$$\alpha = \ln\left(\frac{Q}{4\pi ktv}\right)$$

The expression α includes all the parts of equation 4 not in the exponential term, and being logarithmic does not vary nearly so rapidly as do the quantities t, v, Q and k themselves. It can be seen that the square root term, which allows for the effect of heat conduction, is not simply a constant to be subtracted from $\frac{x}{t}$ in the case of slow sap speeds and ignored in the case of faster flow. In fact this "correction term" increases with increasing flow rate.

Equation 9 can be written in another way:

$$x = Vt + \sqrt{4\alpha kt}$$

which shows the separate effects of convection and conduction more clearly. It gives the distance, x cm which a temperature rise of v° C has reached after t secs. Convection has accounted for a distance Vt as expected, but conduction has added a distance roughly proportional to $\sqrt{t}$. The value of α decreases with the time, t, until it eventually becomes negative at which stage there is no real value for x. This is because the heat pulse has become so diffused that even at its center the temperature rise is less than the threshold temperature rise, v° C.

When $\frac{x}{t}$ is plotted against heat-pulse velocity, V, using equation 9 one obtains curves such as those in figure 7, which are concave towards the V axis. It is interesting that when Huber plotted his "uncorrected speed," $\frac{x}{t}$ (using his "compensation method"), against the flow rate in drops/sec he found in most cases a similar concavity. Huber indicated as a possible explanation, the increase in convecting area with increasing flow rate, but he did not verify quantitatively that this effect was sufficient to account for the curvature. It is not even certain without further investigation that Huber's assumption, that the time of "lower reversal" in his compensation method corresponds to a time of first onset at the downstream junction, is justified. But if this is correct, as seems quite likely, then I consider it almost certain that the main reason for the curvature lies in the variable correction term in equation 9. That Huber himself was unconvinced of the validity of his correction procedure is shown by the concluding sentence of his discussion, namely: "It is clear that theoretically a similar correction (i.e., subtraction of a constant to allow for heat conduction) is needed for all speed values at 4 cm spacing (of heater and nearest junction), but at higher speeds one can generally refrain from making this correction if results of both methods are not to be directly compared with one another."

Analysis of some of Huber's results relating to hardwoods, on the basis of the present theory which was developed for the case of thermally homogeneous softwoods, shows considerable discrepancies as is to be expected. In particular it is found that the magnitude of the heat pulse has decreased much more than the theory predicts in the 4-cm distance. This is probably due to some or all of the following reasons: heat loss to the outside air, the fact that much of the heat remains as a stationary diffusing pulse in the wood and only a portion is carried onward by convection by the sap streams, and thirdly, loss of heat from these sap streams to the unheated walls of the vessels through which they pass. Further research both experimental and theoretical is required before the correct formulae can be found; in the meantime no exact prediction can be made concerning the value of a in the case of hardwoods, and hence of the correction term to be subtracted from $\frac{x}{t}$ to obtain the heat-pulse velocity. One can only be certain that the values given by Huber as "sap speed" are really an overestimate of the heat-pulse velocity.

One aspect of the analysis of Huber's results adds confirmation to the present theory. The time of "lower reversal" in the case of zero flow leads to a value for the diffusivity, and the theory is applicable to all kinds of wood, or indeed to any material. Huber's figures indicate diffusivities from 0.002 to 0.0044 cm^2/sec, typical values for green wood.

Regarding Dixon's method of measurement (3) one can say that for softwoods in the absence of heat loss the estimate of heat-pulse velocity would be correct, but in the case of heat loss or in hardwoods the correct interpretation is uncertain.

Over and above all this there remains the fact that the actual sap speed exceeds the heat-pulse velocity, in the case of softwoods by perhaps as much as 400 %, but for hardwoods probably by a much smaller amount. It may be that some of Huber's figures are fairly accurate if his overestimate of the heat-pulse velocity should coincide with the excess of sap speed over heat-pulse velocity, but no reliance can be placed on this. His results, of course, remain very valuable as a measure of relative rates of sap flow.

It might be thought that the simplicity of the "first onset" formula, equation 9, would make it more useful in practice than our analysis formulae. With our analysis charts, however, each curve can be analyzed in a few minutes, and this method has the following advantages. In the first place, as previously mentioned, there is no need to measure the quantity of heat in the pulse or to calibrate the thermistor equipment. Secondly, it is possible to find both the heat-pulse velocity and the diffusivity from a single measurement—there is no need to make a measurement with zero flow in order to find the diffusivity. Our present methods allowed an accurate check on the validity of the theory and revealed the non-uniformity of the sap flow discussed earlier in the section on Verification Experiments, which would otherwise have gone unnoticed. There may, however, be occasions when the first onset formula would be useful, such as when a large number of successive measurements are to be made at one measuring point where the variation in apparent diffusivity with heat-pulse velocity has already been found.

Summary

Apparatus incorporating a thermistor to measure temperature rises of less than 0.5° F is used to measure the volume rate of sap flow through an area of a few sq cm in the xylem of a conifer.

The method of measuring sap flow by heat transport is put on a sound theoretical basis, confirmed by experiment. The theory shows that the assumption made by previous workers, that the velocity of a heat pulse through the xylem is identical with that of the sap, is not correct. This finding applies to all trees but the exact mathematical relationship derived here applies only to softwoods, which have a comparatively homogeneous xylem.

The present experimental method gives a measure of both the heat conduction and the convection (heat-pulse velocity) from the temperature-time curve of a single heat pulse. If only relative sap flow rates are required, the heat-pulse velocity is an adequate measure, and the only injury to the tree consists in drilling two fine holes. If, however, the actual sap flux in cc/sq cm/hr is desired, a sample of the sapwood must be removed to measure its basic density and moisture content. With the thermistor spaced 1.5 cm from the heater this sap flux is an average over an area about 1.5 cm to 2 cm across, centered on the thermistor.

The apparatus promises to be a useful tool in sap flow research generally. The present experiments, for instance, which were designed simply to verify the theory, have shown the degree of dispersion in the rate of sap flow and the extent of the change in flow on severing the sap streams.

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Appendix

I. Other Analysis Formulae: If on p. 387 the times t_1 to t_4 are chosen so that:

$$\frac{t_2 - t_1}{t_1 t_2} = \frac{t_4 - t_3}{t_3 t_4} \text{ and } t_2 = t_3$$

i.e., if

$$\frac{1}{t_1} + \frac{1}{t_4} = \frac{1}{t_2} + \frac{1}{t_3} = \frac{2}{t_2},$$

the following solutions are obtained:

$$V = 60r\sqrt{\frac{\log_{10}\left(\frac{v_1 t_1 v_4 t_4}{v_2^2 t_2^2}\right)}{t_2\left\{t_4 \log_{10}\left(\frac{v_1 t_1}{v_2 t_2}\right) - t_1 \log_{10}\left(\frac{v_2 t_2}{v_4 t_4}\right)\right\}}} \text{ cm/hr} \quad (10)$$

$$k = \frac{1.8095 r^2 (t_2 - t_1)(t_4 - t_1) \times 10^{-3}}{t_1 t_2\left\{t_1 \log_{10}\left(\frac{v_2 t_2}{v_4 t_4}\right) - t_4 \log_{10}\left(\frac{v_1 t_1}{v_2 t_2}\right)\right\}} \text{ cm}^2/\text{sec}$$

where again t is in minutes.

V and k can thus be obtained in terms of ratios of the temperature rises at three times such that the middle time is either the arithmetic mean or the harmonic mean of the other two.

If the point of maximum temperature rise (v_m, t_m) is used, only one other point of the curve is required. For, by differentiating equation 4 with respect to t and equating the result to zero, we get:

$$4kt_m = x^2 + y^2 - V^2 t_m^2 \quad (11)$$

Substituting $t_1 = t_m$ and $t_2 = pt_m$, where p is any number, in equation 5:

$$\ln\left(\frac{v_m}{pv_2}\right) = \frac{1-p}{p} \times \frac{x^2 + y^2 - pV^2 t_m^2}{4kt_m} \quad (12)$$

The solution of the simultaneous equations 11 and 12 is:

$$V = \frac{60r}{t_m}\sqrt{\frac{2.303 \log_{10}\left(\frac{v_m}{pv_2}\right) + \frac{p-1}{p}}{2.303 \log_{10}\left(\frac{v_m}{pv_2}\right) + p - 1}} \text{ cm/hr} \quad (13)$$

$$k = \frac{r^2}{240pt_m} \times \frac{(p-1)^2}{2.303 \log_{10}\left(\frac{v_m}{pv_2}\right) + p - 1} \text{ cm}^2/\text{sec}$$

where t_m is in minutes.

Alternatively, the two values of v may be chosen in a particular ratio. If $v_1 = nv_m$ we have:

$$V = \frac{60r}{t_m}\sqrt{\frac{2.303 \log_{10}\left(\frac{t_m}{nt_1}\right) + 1 - \frac{t_m}{t_1}}{2.303 \log_{10}\left(\frac{t_m}{nt_1}\right) - 1 + \frac{t_1}{t_m}}} \text{ cm/hr} \quad (14)$$

$$k = \frac{r^2}{240t_m} \times \frac{\frac{t_m}{t_1} + \frac{t_1}{t_m} - 2}{2.303 \log_{10}\left(\frac{t_m}{nt_1}\right) - 1 + \frac{t_1}{t_m}} \text{ cm}^2/\text{sec}$$

where t is in minutes.

Formulae 13 and 14 are not as accurate as 6 and 10 as the point of maximum temperature rise cannot be determined very accurately, especially at slow sap speeds.

II. A Method for Slow Rates of Flow: If it is desired to distinguish accurately between rather slow rates of flow (V less than 10 or 15 cm/hr) and definitely zero flow, a very sensitive system is obtained by recording the temperature at two points at equal distances above and below the heater. If v_1 and v_2 are now the temperature rises at time t at (x_1, y_1) and (x_2, y_2) respectively, then:

$$4kt \ln\left(\frac{v_1}{v_2}\right) = (x_2^2 + y_2^2) - (x_1^2 + y_1^2) + 2Vt\,(x_1 - x_2) \quad (15)$$

If now $x_2 = -x_1$ and $y_2 = -y_1$, we have:

$$V = \frac{k}{x_1} \ln\left(\frac{v_1}{v_2}\right) \text{ cm/sec}$$

Thus, if r is the distance between the heater and each temperature measuring probe, and θ is the angle between the direction of flow and the line of probes and heater,

$$V \cos\theta = \frac{8289k}{r} \log_{10}\left(\frac{v_1}{v_2}\right) \text{ cm/hr} \quad (16)$$

In this case the measurement gives the component of the sap speed along the heater probe direction, whereas the previous formulae for a single probe, in which x and y occur only in the form $x^2 + y^2 = r^2$, give the magnitude of V but no precise information about the direction of flow. As the probe moves further from the x-axis the effect is simply to reduce the v-scale of the (v, t) curve without altering its shape. This is shown by putting $x_1^2 + y_1^2 = x_2^2 + y_2^2$ in equation 15; the resulting equation does not contain t, showing that at any instant the temperatures at two points equidistant from the heater are always in the same ratio.

Equation 16 is useful for ratios of v_1 to v_2 up to about 20, corresponding to $V \cos\theta = 18.0$ cm/hr when r = 1.5 cm and k = 0.0025 cm²/sec. To use this system the apparatus was modified to record either v_1 (as usual) or the difference, $v_1 - v_2$. As v_1 is recorded the output is occasionally switched to ($v_1 - v_2$), thus checking that the ratio v_1/v_2 is constant with time. The value of k is found using the previous formulae, and used in equation 16 to obtain V cos θ.

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IDENTIFICATION AND ESTIMATION OF CATABOLIC PATHWAYS OF GLUCOSE IN FRUITS [1,2]

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The catabolism of glucose and its breakdown products in plants has recently undergone intensive studies in many laboratories (1). Glucose is believed to be utilized for respiratory functions mainly by way of the Embden-Meyerhof-Parnas (EMP) glycolysis and to some extent via the pentose phosphate pathway (2, 6). On the other hand, information on the overall catabolism of glucose in fruit is rather limited although the operation of the tricarboxylic acid cycle (TCA) process, which presumably plays an important role in the catabolism of acetate and pyruvate, has been demonstrated in tomato and pepper (4, 7, 10). In the present work, studies have been extended to include the identification and estimation of pathway participations in glucose catabolism of intact fruits. Using the radiorespirometric method of Wang et al (11), the occurrence of an oxidative pathway involving a preferential oxidation of C-1 of glucose was detected in four varieties of fruits tested. Quantitative evaluation of pathway participations in green mature tomatoes revealed that as much as 84 % of the catabolized glucose was routed via the EMP glycolytic pathway in conjunction with the TCA processes.

Materials and Methods

Fruits: The tomato, cucumber, lime and orange fruits used in the present experiments were obtained from the local market. Specimens for each experiment were selected on the basis of uniformity in size and degree of maturity. In the case of tomato experiments mature fruit (grown to full size) of the Michigan variety furnished by the Field and Bagley greenhouse, Salem, Oregon, were picked immediately prior to the experiments.

Carbon-14 Labeled Substrates: Glucose-1, -2, and -6-C^{14} were obtained from the National Bureau of Standards through the kind cooperation of Dr. H. S. Isbell. Glucose-U-C^{14} was purchased from Tracerlab Inc. Glucose-3(4)-C^{14} was prepared in this laboratory according to the method of Wood et al and was reported to be labeled almost exclusively (97 to 98 %) on carbon atom 3 and 4 (12).

Administration of Labeled Substrate: Aqueous solution of labeled glucose was introduced into the fruit by one of two methods. In the qualitative survey of the occurrence of the direct oxidative pathway in various fruits, a cylindrical well (4.5 mm diameter and 25 mm in depth) was bored into the center of the test fruits, into which was introduced 0.2 ml of the solution containing 0.50 mg of labeled glucose having a radioactivity of 0.5 to 1.0 μc. The well was then sealed with the aid of paraffin. Inasmuch as the area of the well was defined, it is reasonable to believe that in each variety of fruit tested, the labeled substrate was exposed to a constant area of fruit tissue. Test experiments designed for evaluation of the validity of this method of administering the substrate revealed that results obtained with fruits of a given variety were reproducible within 15 % and is, therefore, considered to be satisfactory for qualitative studies.

In the case of quantitative estimation of pathways in tomatoes the substrate solution was introduced into fruit, selected to have weights very close to each other, by means of a modified vacuum infiltration

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