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Kinetics of C-14 Translocation in Soybean

III. THEORETICAL CONSIDERATIONS[1]

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ABSTRACT

Based largely on data from soybean, some mathematical models are derived to describe the transport kinetics of ^{14}C-photosynthate. The effects of leaf size, leaf shape, and translocation velocity on the rate of tracer efflux from the leaf are considered, and it is shown that the duration of these effects will approximate the time required for tracer to reach the petiole from the farthest point of the leaf. This duration is designated as the "kinetic size" of the leaf. Although its effect will be slight in the case of soybean (about 2 to 3 minutes), a considerable effect of the kinetic size will be found in the case of large leaves, or when the translocation velocity is low.

Source pool kinetics in soybean are described by a two-compartment model, one compartment representing a photosynthetic compartment and the second (the source pool) a nonphotosynthetic compartment next to the veins. The kinetics in the petiole are approximated by a two-compartment model representing the translocation stream and tissues outside the translocation stream. A combination of the models predicts fairly accurately the translocation kinetics observed in soybean.

The models are compared with others in the literature. Although the assumptions are in substantial agreement with those made by Evans, Ebert, and Moorby, they are inconsistent with the model based on the movement of transcellular strands presented by Canny and Phillips.

The use of radioactive tracers in translocation studies has encouraged the development of several mathematical models of translocation (5, 6, 12, 17). Since, at least in some cases, the proposed theories for phloem transport would be expected to result in different kinetic observations, these models have often been concerned largely with mechanisms in the stem which would account for the data obtained there. With the exception of Geiger and Swanson's work (10), experimental data for tracer kinetics in the leaf were not utilized in the models, which relied to varying degrees on hypothetical rates of tracer efflux from the leaf (or, in the case of Spanner and Prebble's experiments [17], from a ^{137}Cs source applied directly to the stem) to solve equations for the stem. However, most evidence indicates that the kinetics in the stem are determined primarily by the rate of tracer efflux from the leaf (8). In their work with sugar beet, Geiger and Swanson met with conspicuous success in their mathematical treatment of translocation (11) by paying close attention to the kinetics of ^{14}C-sucrose in the source leaf (10). Nevertheless, the over-all kinetics of translocated compounds in the source leaf are not necessarily an indication of their rate of efflux from the leaf. In at least some cases, compartmentation may play a significant role. The soybean leaf, in particular, has a unique layer of cells in the mesophyll (7) which probably interposes an essentially nonphotosynthetic compartment between the photosynthetic cells and the veins. Also, as several workers have realized, the fact that a leaf has a finite size means that its size and shape and the velocity of translocation may have important effects on the kinetics of tracer efflux from it.

The following mathematical considerations of translocation are an attempt to provide quantitative treatment of some of these factors, using data from the previous two papers (8, 9) as a guide. Calculations are also made for the expected pressure drop for a simple mass flow translocation mechanism in soybean.

EFFECTS OF LEAF SIZE, LEAF SHAPE, AND TRANSLOCATION VELOCITY ON EFFLUX OF RADIOACTIVE TRANSLOCATE FROM LEAVES

The approach followed in constructing these models largely follows the principles outlined by Bird, Stewart, and Lightfoot (2). Emphasis will be placed on the assumptions made for the models, since the equations are only shorthand statements of these assumptions.

Model for Linear, Parallel-veined Leaf. The geometry for this model is shown in Figure 1. (Note that the orientation of coordinates will cause some quantities, including velocity, to assume negative values.) The translocation stream is assumed to be continuous and is bordered by a source pool which supplies the translocate. Assumption of a continuous translocation stream rather than discrete veins is a mathematical necessity but will not detract from the accuracy of the final solution if the leaf area considered is large in comparison to the distance between veinlets. The "source pool" is located in cells immediately surrounding the sieve tubes and does not include the photosynthetic mesophyll.

To solve the equations for an isotopic unsteady state, it is necessary to know the variation of the cross-sectional area of the translocation stream within the leaf. If it is assumed that all areas of the leaf export translocate at an equal rate, then the cross-sectional area of the translocation stream must increase with distance down the leaf, or either the density of the translocate or the velocity of the stream must increase. It is readily apparent from the anatomy of a leaf that the cross-sectional area of the phloem increases. For this, and for other reasons to be mentioned, the

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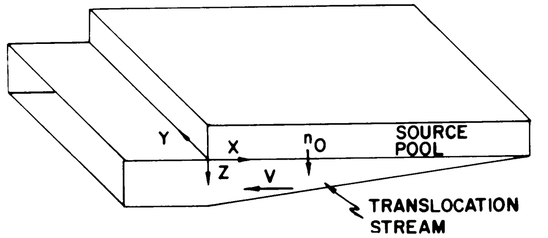

FIG. 1. Model for a linear leaf.

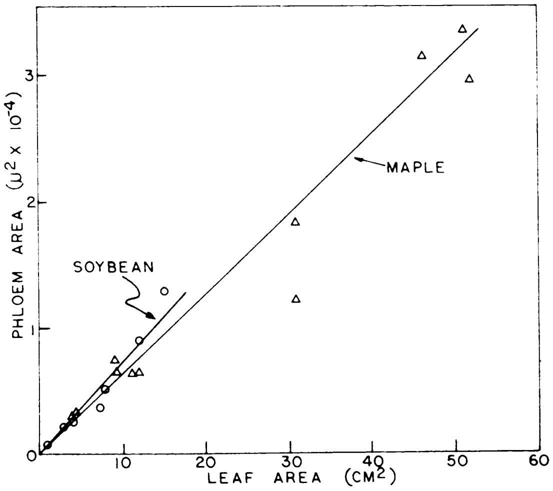

FIG. 2. Relationship of the cross-sectional phloem area to leaf area "upstream" from that point in soybean and maple leaves.

density and velocity have been assumed to be constant throughout the translocation stream.

With these assumptions, the depth, z, of the translocation stream may be expressed as a function of x, the distance from the petiole, by the equation

$$z = \frac{(x - L)n_o}{\rho V} \tag{1}$$

where L = the length of the leaf (cm); n_o = flux of translocate into the translocation stream from the source pool (a constant, g cm^{-2} min^{-1}); ρ = density of translocate within the translocation stream (a constant, g cm^{-3}); V = velocity of the translocation stream (a constant, cm min^{-1}).

The assumption of a constant velocity is an important point for this model and has been discussed at length earlier (8). The assumption that all areas of the leaf contribute equal amounts of translocate (*i.e.*, n_o is constant) would seem to be the most reasonable possibility, given uniform environmental conditions and anatomical uniformity throughout a given leaf. The question of a constant translocate density can only be referred, albeit indirectly, to observations from the stem, where the density changes but little with distance (19).

Equation 1 states that the cross-sectional area of the translocation stream is proportional to the leaf area which exports translocate to it. It can be seen from the measurements plotted in Figure 2 that this proposed proportionality does exist, at least between the phloem area and leaf area. (Sieve tubes occupied about 20% of the phloem area.) The slope of the graph indicates that each square centimeter of leaf area is drained by 740 μ^2 of phloem, or by 148 μ^2 of sieve tubes. However, although this relationship held within the leaf itself, the cross-sectional area of phloem in the soybean petiole, which supported a leaf of 36.1 cm^2, was 33,500 μ^2, or 928 μ^2 of phloem per square centimeter of leaf surface. Either the proportion of sieve tubes is different there, or there is a real increase in the cross-sectional area of the translocation stream as it passes out of the blade into the petiole.

We can now consider the isotopic unsteady state resulting from the introduction of radioactive tracer into the source pool. A mass balance for tracer, R, entering and leaving an incremental volume of the translocation stream, $z\Delta x\Delta y$, may be written as

> Rate of accumulation of R in $z\Delta x\Delta y$ = flow of R in via the translocation − flow of R out via the translocation stream + transport of R into the stream from the source pool − removal of R from the translocation stream

The rate of tracer loss from the translocation stream is apparently only very slight (8) and will be assumed here to be negligible. The verbal statement above can then be written as

$$\frac{\Delta\rho_R}{\Delta t}(z\Delta x\Delta y) = \Delta y(zn_{Rx}\big|_x - zn_{Rx}\big|_{x+\Delta x}) + n_{Ro}\Delta x\Delta y \tag{2}$$

where ρ_R = density of R in the translocation stream (g cm^{-3}); n_{Rx} = flux of R in the x-direction (read $n_{Rx}\,|_x$ as "n_{Rx} evaluated at x") (g cm^{-2} min^{-1}); n_{Ro} = flux of R from the source pool (g cm^{-2} min^{-1}). If diffusion of R is neglected, $n_{Rx} = \rho_R V$. The partial differential equation for this model is obtained by substituting equation 1 for z and taking the limit as Δx, Δy, and Δt approach zero.

$$\frac{\partial\rho_R}{\partial t} = \frac{\rho V n_{Ro}}{n_o(x - L)} - V\frac{\partial\rho_R}{\partial x} - \frac{V\rho_R}{(x - L)} \tag{3}$$

Equation 3 can be solved by using Laplace transforms and applying the boundary condition $\rho_R(L, t) = 0$. The solution is

$$\rho_R = \frac{\rho V}{n_o(x - L)}\left[\int_0^t n_{Ro}(u)\,du - U\left(t - \frac{x - L}{V}\right)\int_0^{t-[(x-L)/V]} n_{Ro}(u)\,du\right] \tag{4}$$

where u is a dummy variable of integration and $U\left(t - \frac{x - L}{V}\right)$, the unit step function, is defined as

$$U(t - a) = \begin{cases} 0, & t < a \\ 1, & t \geq a \end{cases}$$

In this particular case, $a = (x - L)/V$. Since we are interested in the efflux of tracer from the leaf (*i.e.*, $\rho_R(0, t)$), this becomes

$$\rho_{RP} = \frac{-\rho V}{n_o L}\left[\int_0^t n_{Ro}(u)\,du - U\left(t + \frac{L}{V}\right)\int_0^{t+(L/V)} n_{Ro}(u)\,du\right] \tag{5}$$

where $\rho_{RP} = \rho_R(0, t)$.

Since the equation has been derived for any function of n_{Ro} which is dependent only on time, the effects of leaf shape and size can be considered independently of the factors which affect the source pool kinetics. This is a great advantage in considering the many possible factors which might affect the rate of tracer efflux from the leaf, and it is a consequence of the assumption that there is no loss of translocate from the translocation stream.

The assumptions made in deriving this equation are emphasized because the model is only as valid as the assumptions, and because much of the work presented in the preceding papers (8, 9) was aimed at determining their validity or at establishing an experimental value for n_{Ro}. To provide a complete and convenient reference to these assumptions, they are: (*a*) chemical steady state; (*b*) ρ = constant; (*c*) no isotope effect; (*d*) negligible diffusion; (*e*) n_o = constant; (*f*) $v_x = V$ (constant); $v_y = v_z = 0$; (*g*) no removal of translocate from the translocation stream. Similar assumptions will be made in deriving the other two models.

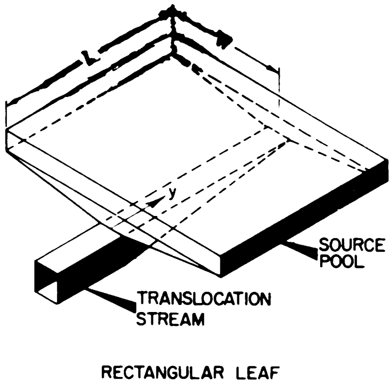

FIG. 3. Model for a rectangular leaf.

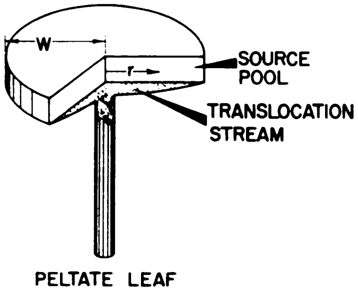

FIG. 4. Model for a peltate leaf.

Model for a Rectangular Leaf. The model for a rectangular leaf, shown in Figure 3, consists essentially of two linear leaf models at right angles to a central channel (analogous to a midrib). The contribution of tracer to the central channel by each of the two "side leaves" is given by equation 5, which can be used in deriving the partial differential equation for the tracer kinetics in the central channel. In principle this may be done for a leaf of any shape, but in practice the resulting equations for any but a rectangular shape do not have a ready solution.

The partial differential equation for this model may be derived by a process similar to that used above for a linear leaf, and is

$$\frac{\partial \rho_R}{\partial t} = \frac{\rho V^2}{n_o W(L - y)} \cdot \left[\int_0^t n_{Ro}(u)\, du - U\left(t + \frac{W}{V}\right) \int_0^{t+(W/V)} n_{Ro}(u)\, du\right] - V \frac{\partial \rho_R}{\partial y} - \frac{\rho_R V}{(y - L)} \tag{6}$$

where W = the distance from the central channel to the edge of the leaf (a constant, cm); L = the length of the leaf (a constant, cm); y = distance along the central channel, measured from the petiole (cm); V = velocity of the translocation stream, assumed to be the same as that in the "side leaves" (cm min^{-1}). The solution, evaluated at $y = 0$, is

$$\begin{aligned} \rho_{RP} = \frac{\rho V^2}{n_o WL} \Bigg[& \int_0^t \int_0^u n_{Ro}(m)\, dmdu \\ & - U\left(t + \frac{W}{V}\right) \int_0^{t+(W/V)} \int_0^u n_{Ro}(m)\, dmdu \\ & - U\left(t + \frac{L}{V}\right) \int_0^{t+(L/V)} \int_0^u n_{Ro}(m)\, dmdu \\ & + U\left(t + \frac{L+W}{V}\right) \int_0^{t+[(L+W)/V]} \int_0^u n_{Ro}(m)\, dmdu \Bigg] \end{aligned} \tag{7}$$

Model for a Peltate Leaf. The model (Fig. 4) is a similar to that for the linear leaf except the equations are derived in a cylindrical coordinate system. The partial differential equation that describes this model is

$$\frac{\partial \rho_R}{\partial t} = \frac{2r\rho V n_{Ro}}{(r^2 - W^2) n_0} - V \frac{\partial[\rho_R (r^2 - W^2)]}{(r^2 - W^2)\partial r} \tag{8}$$

where W = the radius of the leaf (cm); r = distance from the center of the leaf (cm). The general solution, evaluated at $r = 0$ for ρ_{RP}, is

$$\begin{aligned} \rho_{RP} = \frac{2\rho V^2}{n_0 W^2} \Bigg\{ & \int_0^t \int_0^u n_{Ro}(m)\, dmdu - U\left(t + \frac{W}{V}\right) \\ & \cdot \left[\int_0^{t+(W/V)} \int_0^u n_{Ro}(m)\, dmdu - \frac{W}{V} \int_0^{t+(W/V)} n_{Ro}(u)\, du\right] \Bigg\} \end{aligned} \tag{9}$$

COMPARISON OF EFFECTS OF LEAF SIZE, LEAF SHAPE, AND TRANSLOCATION VELOCITY

For this purpose the following values were chosen: leaf area = 24 cm^2; $V = -1.0$ cm min^{-1}; n_o = constant (unknown) for all leaves; linear leaf: $L = 10$ cm; rectangular leaf: $L = 6$ cm, $W = 2$ cm; peltate leaf: $W = 2.8$ cm. These are roughly representative of several experimental plants, including soybean. Since all the models have the same leaf area, n_o and V, the cross-sectional areas of the translocation streams at the petioles will be the same and it will suffice to compare ρ_{RP}'s or a quantity proportional to it.

The tracer content of the source pool will be assumed to increase linearly with time, so $n_{Ro} = \kappa t$, where κ is a constant. For the sake of simplicity κ will be chosen to be unity, and it simply becomes a conversion factor to keep the equations dimensionally correct (*i.e.*, $\kappa = 1$ g cm^{-2} min^{-2}). By substituting the above values into equations 5, 7, and 9, the following solutions are obtained:

Linear leaf:

$$\frac{n_o \rho_{RP}}{\kappa \rho} = \begin{cases} \dfrac{t^2}{20}, & t < 10 \\ t - 5, & t \geq 10 \end{cases}$$

Rectangular leaf:

$$\frac{n_o \rho_{RP}}{\kappa \rho} = \frac{1}{72} [t^3 - U(t - 2)(t - 2)^3 - U(t - 6)(t - 6)^3 - U(t - 8)(t - 8)^3]$$

For $t \geq 8$, this simplifies to

$$\frac{n_o \rho_{RP}}{\kappa \rho} = t - 4$$

Peltate leaf:

$$\frac{n_o \rho_{RP}}{\kappa \rho} = \begin{cases} \dfrac{t^3}{23.52}, & t < 2.8 \\ t - 1.87, & t \geq 2.8 \end{cases}$$

These equations are plotted in Figure 5. It is readily apparent, both from the equations and from the graph, that there is only a brief effect of leaf size on the rates of tracer efflux, and only slight differences among the leaf shapes. After a brief time the rate of efflux largely reflects the kinetics of the source pool. Since it takes a finite time for translocation to pass from its point of origin to the petiole, there is an exponential rise during the first few minutes. The duration of this rise is directly related to the time it

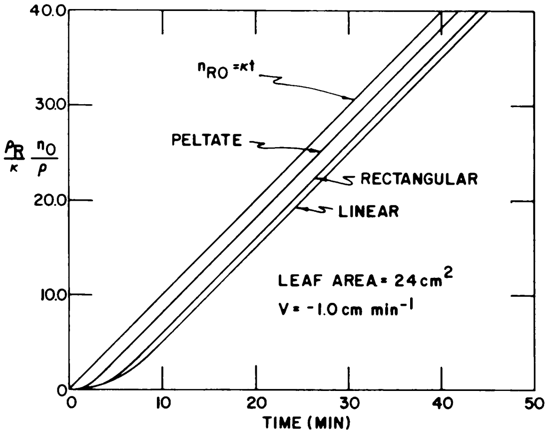

FIG. 5. Theoretical curves for the tracer efflux from linear, rectangular, and peltate leaf models when leaf shape is the only variable, and $n_{Ro} = \kappa t$. (n_{Ro} is not drawn to the same scale as the efflux curves.)

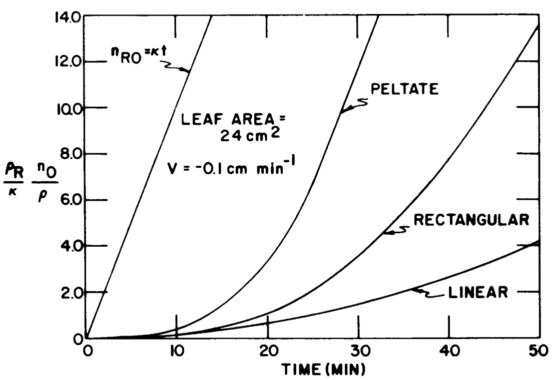

FIG. 6. The effect of increasing the kinetic sizes of the models. Theoretical curves for the tracer efflux from linear, rectangular, and peltate leaf models when leaf shape is the only variable, and $n_{Ro} = \kappa t$. (n_{Ro} is not drawn to the same scale as the efflux curves.)

takes for translocate originating at the farthest part of the leaf to reach the petiole. This time is an important parameter in all of the models and might be referred to as the "kinetic size" of the leaf. Obviously the kinetic size of the soybean leaf is not enough to account for the 20-min exponential rise in the rate of tracer efflux from the leaf during steady state feeding experiments. This is especially true when one considers that the velocity in the leaf is probably more than twice as great as that assumed for the present models (8).

However, if the velocity is -0.1 cm min^{-1}, the effects of both leaf size and shape are quite marked (Fig. 6). Similar effects would result from an increased leaf area since this, too, would increase the kinetic size of the models.

^{14}C KINETICS IN SOYBEAN

Source Pool Kinetics in Soybean. The model tentatively adopted to describe the source pool kinetics assumes that sucrose is produced in a photosynthetic compartment (the palisade and spongy parenchyma) and migrates through a second, nonphotosynthetic compartment (paraveinal mesophyll, border parenchyma, and phloem parenchyma) to the veins (9). On the basis of the relative volumes of these tissues in the leaf, the turnover time of the second compartment will be taken as 15% of the first. Since some sucrose turnover apparently results from causes other than translocation (9), the model cannot be an entirely accurate one. It nevertheless accounts for the main features of ^{14}C translocation kinetics in soybean.

If the photosynthetic compartment is pulse labeled, its ^{14}C kinetics will be described (16) by the equation

$$R_1 = R_o e^{-kt/S_1} \tag{10}$$

where R_1 = dpm in the first (*i.e.*, the photosynthetic) compartment; R_o = dpm in the first compartment at $t = 0$; k = transport rate from the compartment (g min^{-1}); S_1 = compartment size (g). The differential equation for the second compartment is

$$\frac{dR_2}{dt} = k(R_1/S_1 - R_2/S_2) \tag{11}$$

If T is defined as the turnover time, S/k, then the solution to equation 11 is

$$R_2 = \frac{R_o S_2}{S_1 - S_2}[e^{-t/T_1} - e^{-t/T_2}] \tag{12}$$

Equation 12 describes the kinetics in the nonphotosynthetic compartment. When turnover times of 77 and 11 min are assigned to the photosynthetic and nonphotosynthetic compartmetns, respectively (9), the curves shown in Figure 7 describe the kinetics for the model. The curve for the smaller compartment, which is taken to represent the source pool kinetics, is almost identical to that following pulse labeling for sterol glucoside (Reference 9, Fig. 5) and is also very similar to that for ^{14}C kinetics in the soybean petiole (Reference 8, Fig. 12).

Kinetics in the Stem and Petiole. If the assumptions made for the leaf models are applied to movement of tracer in the stem, the partial differential equation describing this movement will be

$$\frac{\partial \rho_R}{\partial t} = -V\frac{\partial \rho_R}{\partial x} \tag{13}$$

In this model the origin of the x-axis is at the point where the petiole joins the leaf and extends in the positive direction from the leaf, down the conducting tissues. If $\rho_R(x, 0) = 0$ and $\rho_{RP}(t)$ is the density of R entering the translocation stream at the petiole, then the solution to equation 13 is:

$$\rho_R = U\left(t - \frac{X}{V}\right)\rho_{PR}\left(t - \frac{X}{V}\right) \tag{14}$$

A graph of ρ_R *vs.* x will be the mirror image of $\rho_{RP}(t)$, except that the origin will be at $x = V/t$ and will be "stretched" or "compressed" along the x-axis, depending on whether V is greater or less than 1 cm min^{-1}. Although equation 14 should offer a fairly

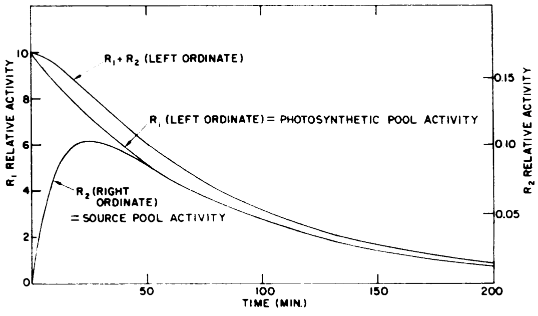

FIG. 7. Solutions to a two-compartment model for the source pool kinetics in soybean. R_1 = radioactivity in the photosynthetic compartment, which is assumed to be pulse labeled, with a turnover time of 77 min. R_2 = radioactivity in the paraveinal mesophyll (assumed to be very close to the kinetics in the source pool) with a turnover time of 11 min.

accurate description of tracer kinetics in the translocation stream itself, it cannot be applied after long periods of time to the kinetics in the stem as a whole because of slow leakage from the translocation stream. Over relatively long periods a significant amount of activity would accumulate outside the sieve tubes.

The data on relative specific activities of leaf and petiolar sucrose suggested that loss of ^{14}C-sucrose from the translocation stream might be accounted for by a two-compartment model (8). The kinetics of one compartment (the translocation stream) are assumed to be determined by the rate of tracer efflux from the leaf, and the second compartment (the surrounding tissues) receives sucrose slowly and reversibly from the first. In solving the equations, however, backflow of tracer from the second compartment to the first will be ignored, since the slow turnover time which must be assigned to the second compartment will make this tracer contribution negligible in comparison with that coming from the leaf. Although the equations will be derived for that part of the petiole immediately outside the leaf, they will apply at any distance X along the translocation stream after a time lag of X/V (*i.e.*, after the tracer reaches that point).

To simplify the mathematics, the effect of leaf size will be ignored since its kinetic size is so small, and the equation describing the kinetics in the source pool (equation 12) will be applied to the translocation stream. The amount of sucrose in the translocation stream will be taken as twice that in the surrounding tissues (8). Under these conditions the differential equation for the sucrose outside the translocation stream will be

$$\frac{dR_3}{dt} + \frac{k_3R_3}{S_3} = \frac{k_3R_0}{S_1 - S_2}\left[e^{-t/T_1} - e^{-t/T_2}\right] \qquad (15)$$

where k_3 = transport rate from the translocation stream to the stationary pool and *vice versa* (g min^{-1}); R_3 = dpm in the stationary sucrose pool; S_3 = total sucrose in the stationary pool (g); T_1 = turnover time in the photosynthetic sucrose pool (min); T_2 = turnover time in the source pool (min). The solution to equation 15 is

$$R_3 = \frac{k_3R_0}{S_1 - S_2}\left[\frac{(e^{-t/T_1} - e^{-t/T_3})}{T_3^{-1} - T_2^{-1}} - \frac{(e^{-t/T_2} - e^{-t/T_3})}{T_3^{-1} - T_2^{-1}}\right] \qquad (16)$$

Trial calculations showed that the ratio of sucrose specific radioactivity in the leaf to that in the petiole quickly became more than unity unless the turnover time of the sucrose pool outside the translocation stream were appreciably greater than the photosynthetic pool. Accordingly, the turnover time of the stationary pool was chosen to be twice that of the latter. Curves describing the ^{14}C kinetics in the translocating, stationary, and total sucrose pools are shown in Figure 8, where they are compared with data obtained by monitoring the petiole after pulse labeling the leaf (8). The curves for the soybean petiole and total ^{14}C-sucrose are reasonably close considering the approximate nature of the solution for the model. A quite close fit for the first part of the curve would result if the effects of phosphorylated compounds and leaf size were included.

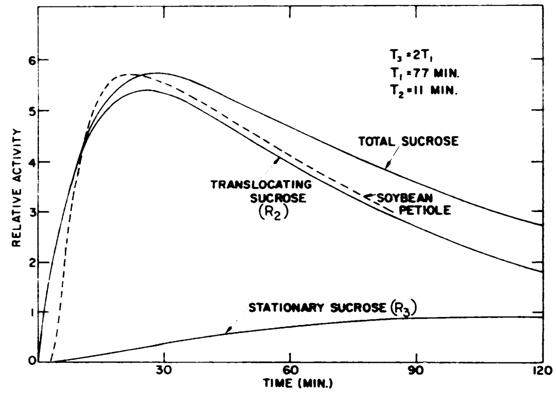

FIG. 8. Solutions to a three-compartment model for the ^{14}C kinetics in a soybean petiole following pulse labeling of the leaf.

AN ESTIMATE OF THE PRESSURE DROP IN SOYBEAN SIEVE TUBES

The sieve tubes in the soybean petiole are about 125 μ long, 20 μ^2 in area, and have sieve plates about 1.5 μ thick with 50 to 70 pores about 0.5 μ in diameter. Since the velocity was approximately 2.5 cm min^{-1} (8), there should be a pressure drop of 0.25 atm cm^{-1} if it is assumed that a pressure-flow mechanism is operative and that the Hagen-Poiseuille equation can be applied. The osmotic potential of a 13% solution (8) would be of the order of 10 atm and so could generate sufficient pressure to cause mass flow at the observed rate in a 30-cm soybean stem. However, the margin between available pressure and that required is not great and the calculation ignores the effect to be expected from strands in the pores, if they are assumed to be stationary. In addition, the pore diameter used must be regarded as the maximum possible (it results in an open area in the sieve plate of 50%). Since the pressure drop is proportional to the fourth power of the radius, even a slightly smaller pore size would increase the calculated pressure drop markedly.

DISCUSSION

Once considered, it is readily apparent that the various times it takes for tracer to reach the petiole from different points of the leaf will have an effect on the rate of tracer efflux from the leaf. The models presented demonstrate that the most important parameter governing this effect is the "kinetic size" of the leaf. In practice it may be difficult to determine the exact kinetic size of a leaf, largely due to ambiguities in the translocation velocity resulting from possible changes in the cross-sectional area of the translocation stream (8). It is apparent, however, that in many cases the kinetic size is too small to affect greatly the kinetics of tracer efflux from the leaf. This is the case in soybean where, with a probable translocation velocity of more than 2.5 cm min^{-1} in the leaf (8), the kinetic size would be only 2 to 3 min. In cases where the leaf may be large (*e.g.*, sugar beet [14]) or where the translocation velocity is low (*e.g.*, willow [3]), the kinetic size would have a considerable effect on the tranlsocation kinetics.

The assumptions made for the kinetic models of translocation in the stem are quite similar to those made by Horwitz (Reference 12, models 1 and 3), Spanner and Prebble (17), and Evans, Evert, and Moorby (6) in that they assume a constant velocity of translocation with irreversible loss from the translocation stream. (In the model presented here, the long turnover time assigned to the stationary sucrose pool will have the effect of making the loss essentially irreversible during short times.) The rate of loss in Spanner and Prebble's model is much greater than for the other models and leads to considerably different kinetic curves. The experimental data to which the model is applied, however, concerned ionic^{135}Cs which had been applied to the petiole. As they point out, cesium cannot be expected to behave in the same physiological manner as the translocate. An equally important consideration, however, is that the system they were studying was in a chemical unsteady state caused by the introduction of cesium. This is very different from the introduction of ^{14}C, via photosynthesis, into a system in a chemical steady state. The loss of cesium from the translocation stream would be expected to be quite high in a chemical unsteady state.

Of Horwitz's models for translocation, the only one which includes a time variable source (model 3) treats the case in which the rate of tracer influx into the stem increases according to the equation $C_o = k(1 - e^{\gamma t})$, where C_o is the concentration of tracer leaving the leaf and k and γ are constants. These kinetics would simulate steady state labeling of a single source pool. Although he rejected this model because it apparently cannot generate the exponential translocation profiles reported at that time, it was treated more completely by Evans *et al.* (6). They showed that, with steady state labeling, the translocation profile in soybean is linear after about the first 25 min. This agrees with data reported in the first paper of this series (8). They suggested that the initial 25-min exponential increase in the rate of tracer influx into the stem is due to different times for the transport of ^{14}C-photosynthate to the translocation system. This is, in fact, essentially the effect produced by the interposition of a nonphotosynthetic compartment (the paraveinal mesophyll) between the photosynthetic parenchyma and the veins.

In order to fit their model with the data, it was necessary to assume a very low rate of loss of translocate from the translocation stream. Under their proposed conditions, about 80% of the translocate (or tracer) would pass through a soybean stem 30 cm long. This loss is so little that, after the tracer front reached there, the kinetics at any point along the stem would be much the same regardless of its position. The greatest difference (20%), existing between the top and bottom of the stem, would not be experimentally noticeable. In the model presented here, which assumes reversible loss of translocate, the loss of tracer over a distance of 30 cm would be about 19%. Again, this is too slight to cause noticeable differences in the kinetics at different points along the stem. In fact, the predicted kinetic differences between this model and that of Evans *et al.* would not be sufficient to rule out one or the other on the basis of present kinetic evidence. In view of the fact that most of the loss occurs as sucrose, which is only slowly metabolized to other compounds (1, 8), and the capacity of phloem to accumulate sucrose (1), the reversible model would seem to be more realistic.

The assumptions made for the above models are considerably different from those made by Canny and Phillips (5), who based their calculations on the proposed bidirectional movement of transcellular strands in sieve tubes. However, their model has several serious difficulties. Canny himself has pointed out that it probably cannot account for observed transport rates (4).[3] In addition, the translocation of ^{14}C-sucrose in soybean, at least, does not follow kinetics which can be accounted for by their model. Since, both after pulse labeling and during steady state labeling, the profile proceeds down the stem with little or no change in shape (8, 13), diffusion kinetics cannot describe the movement (8). According to Canny and Phillip's treatment, the profiles would then presumably be classed as the "wave" type. If leakage from the strands were very slow, there would be no qualitative difference between the kinetics predicted by their model and those predicted by the model presented in this paper or by Evans, Ebert, and Moorby's model. However, since two-thirds of the petiolar sucrose apparently equilibrated very rapidly with exported sucrose, most, if not all, of the sucrose in the sieve tubes must have been in the translocation stream.

From the point of view of tracer kinetics, a bulk flow mechanism with slight loss of translocate from the translocation stream provides a satisfactory basis for a kinetic model. Although a parabolic velocity gradient might exist, radial diffusion would cause the average velocity of all molecules to be the same (6, 18). However, it is questionable whether there was sufficient pressure available for the operation in soybean of a simple pressure flow mechanism like that envisioned by Munch (15).

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APPENDIX: LIST OF SYMBOLS

The notation followed has been adopted almost entirely from "Transport Phenomena," by Bird, Stewart, and Lightfoot (3), and from "Basic Principles of the Tracer Method" by Sheppard (28).

The dimensions of each quantity are indicated after its definition in terms of mass (M), length (L) and time (t). Symbols which appear only once are not listed.

Arabic letters
A = area, L^2
a = specific radioactivity (= R/S), dpm M^{-1}
k = rate of transport between compartments, Mt^{-1}
L = length of a leaf, L
m = dummy variable of integration
n = chemical mass flux, $ML^{-2}t^{-1}$
n_o = chemical mass flux into the translocation stream from the source pool, $ML^{-2}t^{-1}$
n_{Ro} = isotopic mass flux into the translocation stream from the source pool, $ML^{-2}t^{-1}$
n_x = chemical mass flux in the x-direction, $ML^{-2}t^{-1}$
n_{Rx} = isotopic mass flux in the x-direction, $ML^{-2}t^{-1}$
R = radioactivity, dpm
r = radius, L
S = total (chemical) amount of substance in a compartment, M
T = turnover time of a compartment (= S/k), t
t = time, t
u = dummy variable of integration
V = velocity of translocation, Lt^{-1}
W = radius of a peltate leaf model, or the half-width of a rectangular leaf model, L
x = distance along the x-axis, L
y = distance along the y-axis, L
z = distance along the z-axis, L
Greek letters
κ = 1 gm cm^{-2} min^{-2}
π = 3.14159···
ρ = chemical density, ML^{-3}
ρ_R = isotopic density, ML^{-3}
ρ_{RP} = isotopic density as the translocation exits from the leaf, ML^{-3}

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[3] An arithmetic error by Canny and Phillips caused their estimate of the sugar flux (their Fig. 4) for the model to be high by 10-fold.

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