

SOME SIMPLIFIED MATHEMATICAL TREATMENTS OF TRANSLOCATION IN PLANTS¹

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When radioactive tracer techniques began to be used in studies on translocation in plants, experiments of a hitherto unparalleled degree of precision and incisiveness became possible. Many of the results obtained to date with isotopic techniques have merely been a confirmation, in a much more elegant way, of phenomena that had already been rather well established by other methods. But, data from tracer studies have lately been appearing in the literature which permit a much more quantitative evaluation of the translocation process than had previously been possible. The main feature of these data is that there is generally a more or less linear relationship between the logarithm of the radioactivity at any place in the stem and its distance from the region of application (1, 2, 3). In this paper the consequences of a number of simple theories of translocation have been derived mathematically, in order to see which of these theories are plausible and conform to experimental observations. In addition it is hoped that these analyses may make more clear the kinds of experiments necessary to define the character of the translocation process.

1. FLOW THROUGH A PIPE WITH IRREVERSIBLE LOSS THROUGH THE WALLS: At least two extant theories of translocation involve the movement "en masse" of all or a portion of the fluid contained in the sieve tube. These are the theories of protoplasmic streaming in which the movement is actuated by living protoplasm, and pressure flow in which osmotic pressure supplies the motive force (4). The latter theory will be dealt with in more detail in a later section. For the purposes of this model, translocation is visualized simply as involving unidirectional mass flow of the fluid contents of a pipe (the sieve tube column) regardless of the actuating mechanism. The presence of sieve plates will provide an additional obstacle to flow in the pipe, and may be of importance in deciding what actuating mechanism operates, but need not invalidate the use of a pipe as a model for the sieve tube column. Solute may diffuse through the walls of the pipe, but no net transfer of water occurs between the inside and outside of the pipe. Furthermore, although the flow is laminar, as is shown in appendix 1, there is assumed to be sufficient mixing so that concentrations within the pipe are essentially

uniform throughout its cross section. In addition, attenuation of concentration at the front of flow of a solute, continuously injected into the pipe at some point, is assumed to be unimportant. Sufficient mixing might be obtained by diffusion and as a result of the interference to flow presented by the sieve plates.

In order to explain the experimentally observed distribution of radioactivity in short term translocation experiments, we consider the following situation. Suppose that for a distance h somewhere along the pipe, it is surrounded by a steady state concentration C_1 of the radioactive material X , and that K is a first order constant characterizing the rate of transfer of X through the pipe wall in the region h . If the velocity of flow of the fluid in the pipe is v and the pipe cross sectional area is A_p , then the concentration of X in the pipe at the outflow edge of the region h is

$$C_0 = C_1(1 - e^{-\frac{Kh}{A_p v}}). \quad (1)$$

In order to account for X after it leaves the region h , we use the following additional symbols:

x = distance along the pipe from the region h in the direction of flow.

t = time.

C_p = concentration of X in the pipe at any distance x .

C_t = concentration of X in the tissue surrounding the pipe at any distance x .

k = constant for diffusion of X through the pipe wall or a first order chemical reaction rate constant for removal of X from the flowing stream into a bound form.

A_t = cross sectional area of tissue surrounding the pipe.

If there is neither diffusion of X out of the pipe nor net diffusion of water into the pipe, then there will be no attenuation of X concentration in the stem with distance away from the source region h . This obviously does not conform to experimental observations with P^{32} , C^{14} , and K^{42} (1, 2, 3).

However, if X may diffuse out of the pipe and is thereupon chemically bound into a species unable to diffuse back, then C_p will be subject to the following relation:

$$\frac{dC_p}{dx} = -\frac{k}{A_p v} C_p = -\frac{k_1}{v} C_p. \quad (2)$$

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Integrated, this gives:

$$C_p = C_0 e^{-\frac{k_1 x}{v}} \quad (3)$$

The concentration, C_p , in the pipe, therefore, is not time dependent, and fulfills equation 3 from the end of region h to the front of flow of X . Beyond that it is zero.

Therefore, the concentration, C_t (which is in a bound form), in the tissue surrounding the pipe at a distance x , anywhere from region h to the front of flow of X , is given by:

$$C_t = \frac{k}{A_t} C_0 e^{-\frac{k_1 x}{v}} \left(t - \frac{x}{v} \right) = k_2 C_0 e^{-\frac{k_1 x}{v}} \left(t - \frac{x}{v} \right) \quad (4)$$

The total amount of X , then, at any level in the stem from region h to the front of flow is

$$X = A_p C_0 e^{-\frac{k_1 x}{v}} + A_t k_2 C_0 e^{-\frac{k_1 x}{v}} - A_t \frac{x}{v} k_2 C_0 e^{-\frac{k_1 x}{v}}, \quad (5)$$

or

$$X = C_0 e^{-\frac{k_1 x}{v}} \left\{ A_p + k \left(t - \frac{x}{v} \right) \right\}, \quad (6)$$

and

$$\log_e X = \log_e C_0 + \log_e \left\{ A_p + k \left(t - \frac{x}{v} \right) \right\} - \frac{k_1 x}{v} \quad (7)$$

The slope of the curve relating $\log_e X$ and x is

$$\frac{d \log_e X}{dx} = - \frac{k}{v \left(A_p + k \left(t - \frac{x}{v} \right) \right)} - \frac{k}{v A_p}, \quad (8)$$

and for a given value of x , decreases with time at the rate given by:

$$\frac{d^2 \log_e X}{dx dt} = \frac{k^2}{v \left(A_p + k \left(t - \frac{x}{v} \right) \right)^2} \quad (9)$$

The rate of increase of $\log_e X$ with respect to time is

$$\frac{d \log_e X}{dt} = \frac{k}{A_p + k \left(t - \frac{x}{v} \right)} \quad (10)$$

The rate of change of the slope with respect to distance and time in any region of the stem will decrease as this region falls farther behind the front of flow of X (that is, as $(t - x/v)$ increases).

That the formulations resulting from this analysis give a good representation of experimental data can

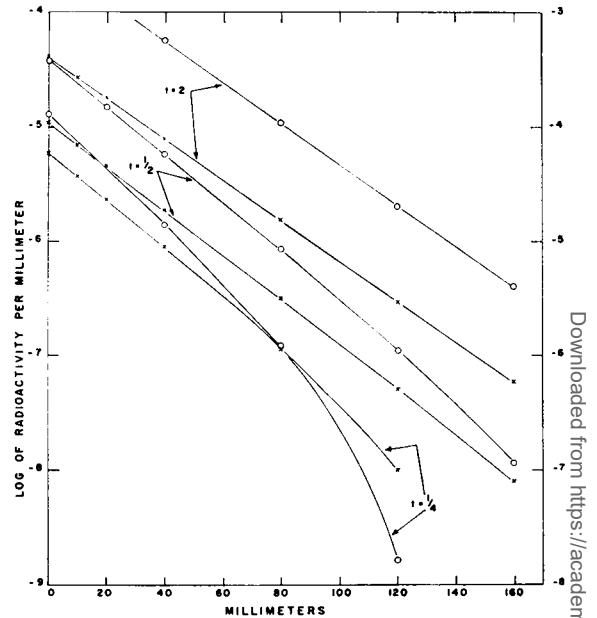


FIG. 1. Comparison of the radioactivity distributions obtained with models 1 and 3. Abscissa is distance along stem in millimeters. The ordinate is radioactivity per mm of stem in units of logarithm to the base 10. The curves through the crosses (\times), referring to the right hand ordinate, are for model 1 with immediate attainment of the steady state in the source region h . They are, respectively, for $\frac{1}{4}$, $\frac{1}{2}$, and 2 hours. The curves through the circles (\circ), referring to the left hand ordinate, are for model 3, with a half time of 24 minutes for attainment of the steady state in the source region h . They are also, respectively, for $\frac{1}{4}$, $\frac{1}{2}$, and 2 hours. Other parameters, applicable to all curves, are $A_p = 0.1 \text{ mm}^2$, $k = 2 \text{ mm}^2/\text{hr}$, and $v = 500 \text{ mm/hr}$.

be seen from figure 1, where equation 6 is plotted on semi-logarithmic coordinates. The following parameters, reasonable for the bean plants used by Biddulph and Cory (3), were assumed: $A_p = 0.1 \text{ mm}^2$, and $v = 500 \text{ mm/hr}$. With a value for k of $2 \text{ mm}^2/\text{hr}$, curves result that are much like those obtained by Biddulph and Cory (3) with P^{32} . The steeper slopes for their curves of P^{32} distribution at short times are partially accounted for in equation 8 from which one would predict a somewhat greater slope at short times. However, one would also expect greater slopes at short times, due to the fact that X is only just beginning to diffuse into the region h around the pipe, and C_1 and therefore C_0 are still rising to their steady state values.

Swanson and Whitney (2) have made some interesting observations on the simultaneous translocation of two radioisotopes which can be interpreted in the light of the formulation developed here. In all cases, apparently, a plot of the logarithm of their radioactivities against distance from the point of application was linear. But whereas the slopes for Cs^{137} and P^{32} , applied simultaneously, were different, those for K^{42} and P^{32} were the same. Equation 8 shows that the

slope is determined by the three parameters k , A_p , and v . There is no need, therefore, to suppose, as Swanson and Whitney apparently did, that a difference in slope necessarily implies a difference in the rate of flow v , since differences in k or A_p can adequately account for it.

However, the data comparing K^{42} and P^{32} cannot be resolved, in the present formulation, without assuming completely different modes of transport for K^{42} and P^{32} , i.e., different A_p 's or v 's or both different. For although the slopes for these two substances remained the same, the rates of increase of the logarithms of their radioactivity with respect to time were different. Therefore, according to equation 10 at least one of the parameters, k , v , or A_p must differ. But since the slopes are the same, equation 8 demands that at least two of these parameters must differ. So either the v 's or the A_p 's or both involved in the transport of potassium and phosphorus must be different.

2. FLOW THROUGH A PIPE WITH REVERSIBLE LOSS THROUGH THE WALLS: This situation is like that of the preceding model except that X is not bound into an inert form upon leaving the flowing stream, but is available for reentry into it. Using the same symbols

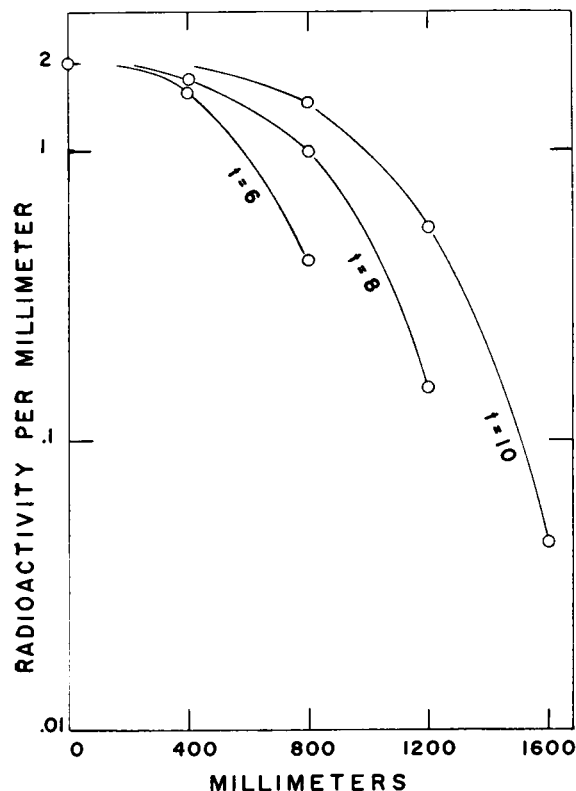


FIG. 2. Distribution of radioactivity with distance according to model 2. Abscissa is distance along stem in millimeters. Ordinate is radioactivity per millimeter along stem in arbitrary units on a logarithmic scale. The curves are for 6, 8, and 10 hours respectively. The other parameters, applicable to all curves, are $k_1 = 1 \text{ hr}^{-1}$, $k_2 = 1 \text{ hr}^{-1}$, and $v = 200 \text{ mm/hr}$.

as before, this can be formulated mathematically in the following way: For the contents of the pipe contained within any element dx , conservation of matter demands that

$$\frac{\partial C_p}{\partial t} = -v \frac{\partial C_p}{\partial x} - \frac{k}{A_p} (C_p - C_t) = -v \frac{\partial C_p}{\partial x} - k_1 (C_p - C_t). \quad (11)$$

The first term on the right side accounts for change in concentration due to flow of fluid in the pipe and the second term for transfer between the inside and outside of the pipe.

For the tissue surrounding the pipe and contained within the element dx

$$\frac{\partial C_t}{\partial t} = \frac{k}{A_t} (C_p - C_t) = k_2 (C_p - C_t). \quad (12)$$

The integration of these equations is far more difficult than the ones for the model with irreversible loss. Fortunately, an essentially similar problem has already been solved for the case of heat transfer between a fluid flowing in a pipe and the walls of the pipe (5). Using these results and the following convenient arbitrary values for the parameters: $k_1 = 1 \text{ hr}^{-1}$, $k_2 = 1 \text{ hr}^{-1}$, and $v = 200 \text{ mm/hr}$, the curves of figure 2 were drawn. They show the distribution of X in the stem after 6, 8, and 10 hours and are obviously far different from experimental curves.

The model with irreversible loss is essentially a special limiting case of the model with reversible loss, and the results of section I can also be obtained from equations 11 and 12. In the case of irreversible loss, they become

$$\frac{\partial C_p}{\partial t} + v \frac{\partial C_p}{\partial x} = -k_1 C_p \quad (13)$$

and

$$\frac{\partial C_t}{\partial t} = k_2 C_p. \quad (14)$$

By introducing two new variables

$$y = \frac{k_1 x}{v} \quad (15)$$

and

$$z = k_2 \left(t - \frac{x}{v} \right), \quad (16)$$

they simplify to

$$\frac{\partial C_p}{\partial y} = -C_p \quad (17)$$

and

$$\frac{\partial C_t}{\partial z} = C_p. \quad (18)$$

Equation 17 integrates to

$$C_p = C_0 e^{-\frac{k_1 x}{v}} \quad (19)$$

By substituting this value for C_p in 18, one obtains

$$C_t = k_2 C_0 e^{-\frac{k_1 x}{v}} \left(t - \frac{x}{v} \right) \quad (20)$$

Equations 19 and 20 are identical with 3 and 4 respectively.

3. FLOW THROUGH A PIPE WITH A TIME VARIABLE SOURCE OF RADIOACTIVITY: In the preceding models, the concentration, C_1 , of the radioactive substance in the source region h surrounding the pipe, was assumed to be constant. Since this is obviously not always true and a non-steady state in the source region at short times was already invoked to explain certain features of the behavior of P^{32} , a quantitative treatment of a non-steady state situation is given here.

The model treated is one that might be useful in analyzing data, such as that of Vernon and Aronoff (1), who illuminated a leaf completely enclosed in an atmosphere containing $C^{14}O_2$ and followed the distribution of the radioactive translocate. The following symbols, in addition to those already defined, are used:

σ = rate of photochemical fixation of CO_2 in the source region h .

λ = isotopic ratio of $C^{14}O_2$.

K = constant for diffusion of C_1 from region h into the pipe.

A_h = average cross sectional area of the region h .

h = length of the pipe within the region h .

Distance is measured from the outflow end of the region h and is positive in the direction of flow.

If we assume that the flowing fluid in the pipe leaches X out of region h at such a slow relative rate that C_1 is essentially constant over the whole length h and that C_1 does not appreciably change in the time h/v , then the following equation holds in the length h :

$$\frac{dC_p}{dx} = \frac{K}{A_p v} (C_1 - C_p) \quad (21)$$

Integration of equation 21 gives:

$$\begin{aligned} C_p &= C_1 \left(1 - e^{-\frac{K}{A_p v}(x+h)} \right) \\ &= C_1 \left(1 - e^{-\frac{K_1}{v}(x+h)} \right), \end{aligned} \quad (22)$$

and at $x=0$

$$C_0 = C_1 \left(1 - e^{-\frac{K_1 h}{v}} \right) \quad (23)$$

The rate of loss of X from region h into the pipe is from equation 23:

$$\nu = A_p v C_0 = A_p v C_1 \left(1 - e^{-\frac{K_1 h}{v}} \right) \quad (24)$$

Or, the rate of decrease in C_1 in the region h due to loss to the pipe is:

$$\nu_c = \frac{A_p v C_1}{A_h h} \left(1 - e^{-\frac{K_1 h}{v}} \right) \quad (25)$$

(By expanding the exponential term in a Taylor's series around zero, it is easily seen that, as should be expected from the physical qualities of the system, $\nu_c \rightarrow C_1 K/A_h$ as $v \rightarrow \infty$.)

The rate of change of C_1 , then, is given by

$$\frac{dC_1}{dt} = \sigma \lambda - \nu_c = \sigma \lambda - \frac{A_p v C_1}{A_h h} \left(1 - e^{-\frac{K_1 h}{v}} \right) \quad (26)$$

Or, introducing the composite constants:

$$A = \frac{A_p}{A_h h} \quad (27)$$

and

$$\gamma = A v \left(1 - e^{-\frac{K_1 h}{v}} \right), \quad (28)$$

we get

$$\frac{dC_1}{dt} = \sigma \lambda - \gamma C_1 \quad (29)$$

Integration of 29 gives

$$C_1 = \frac{\sigma \lambda}{\gamma} \left(1 - e^{-\gamma t} \right) \quad (30)$$

Upon substituting this value for C_1 in equation 23, we get an expression describing how the supply of radioactive material X , for translocation from the source region h , varies with time:

$$C_0 = \frac{\sigma \lambda}{A v} \left(1 - e^{-\gamma t} \right) \quad (31)$$

Now suppose, as in the first model, that X , in the course of flowing down the pipe, is lost irreversibly to the surrounding tissue. Then, the concentration, C_p , will be governed by equation 2, also as in the first model. In the present case, however, there is a time variable boundary condition, and integration of equation 2 gives

$$C_p = \left\{ \frac{\sigma \lambda}{A v} \left(1 - e^{-\gamma \left(t - \frac{x}{v} \right)} \right) \right\} e^{-\frac{k_1 x}{v}} \quad (32)$$

To calculate C_t as a function of x and t integrate

$$\frac{dC_t}{dt} = \frac{k}{A_t} C_p = k_2 C_p, \quad (33)$$

getting

$$\int_0^{C_t(t)} dC_t = k_2 e^{-\frac{k_1 x}{v}} \frac{\sigma \lambda}{A v} \int_{x/v}^t \left(1 - e^{-\gamma \left(\tau - \frac{x}{v} \right)} \right) d\tau \quad (34)$$

and

$$C_t = k_2 e^{-\frac{k_1 x}{v}} \frac{\sigma \lambda}{A v} \left\{ \left(t - \frac{x}{v} \right) - \frac{1}{\gamma} \left(1 - e^{-\gamma \left(t - \frac{x}{v} \right)} \right) \right\} \quad (35)$$

The content of radioactivity at any level in the stem, therefore, from region *h* to the front of flow is:

$$X = A_p C_p + A_t C_t, \tag{36}$$

or

$$X = \left\{ k \left(t - \frac{x}{v} \right) + (1 - e^{-\gamma(t-\frac{x}{v})}) \left(A_p - \frac{k}{\gamma} \right) \right\} \frac{\sigma\lambda}{Av} e^{-\frac{kix}{v}}. \tag{37}$$

Equation 6 of the first model is clearly a limiting case of 37 when the arrival at the steady state is instantaneous, or when $\gamma = \infty$. When there is no loss from the pipe, i.e., when $k = 0$, then 37 reduces to:

$$X = \frac{A_h h \sigma \lambda}{v} (1 - e^{-\gamma(t-\frac{x}{v})}). \tag{38}$$

The slope obtained from plotting equation 37 on semi-logarithmic coordinates is

$$\frac{d \log_e X}{dx} = \frac{\frac{k}{v} + \left(\frac{\gamma A_p}{v} - \frac{k}{v} \right) e^{-\gamma(t-\frac{x}{v})}}{k \left(t - \frac{x}{v} \right) + (1 - e^{-\gamma(t-\frac{x}{v})}) \left(A_p - \frac{k}{\gamma} \right) - \frac{k}{A_p v}}. \tag{39}$$

The effect of the non-steady state situation on the family of curves obtained at various times can be succinctly demonstrated by a consideration of the slope at $x = 0$ and when the source region *h* has attained half its steady state concentration. The time to reach a half of the steady state concentration can be obtained from equation 30 and is $0.693/\gamma$. Upon substituting these values of *t* and *x* in equation 39, and simplifying, one obtains

$$\left(\frac{d \log_e X}{dx} \right)_{x=0}^{t=t_{1/2}} = - \frac{\frac{k + \gamma A_p}{v}}{\frac{0.386k}{\gamma} + A_p} - \frac{k}{A_p v}. \tag{40}$$

Thus during the time when the source region is approaching its steady state, the slope will be greater by an amount that increases with γ , the time constant for approach. However, limits on the effect that γ can exert are imposed by itself, since a larger γ will not only increase the slope but will also decrease the duration of the increased slope by speeding up the approach to the steady state. As $(t - x/v)$ increases, i.e., as the region of the stem under consideration falls farther behind the front of flow, equations 37 and 39 approach the same values as 6 and 8.

These considerations probably preclude an explanation of the available data (1, 3), about attenuation of radioactivity with distance down the stem, that is

based only on the non-steady state and does not make use of loss from the pipe as well. For, assuming a half time for attainment of the steady state of 24 minutes and a value of *v* equalling 500 mm/hr, one finds from equation 38 that, in the first 160 mm of translocation path, the attenuation of radioactivity is mostly well within one order of magnitude between 15 and 30 minutes and is rapidly decreasing. The experimentally observed degree of attenuation, however, is commonly around two to three orders of magnitude for P^{32} (3) and C^{14} (1).

A comparison of the curves obtained with respective half times, for attainment of the steady state, of 24 minutes ($\gamma = 1.73$) and 0 ($\gamma = \infty$) is shown in figure 1. The following additional parameters used are the same for the two curves: $A_p = 0.1 \text{ mm}^2$, $v = 500 \text{ mm/hr}$, $k = 2$. The non-steady state curve obtained at $\frac{1}{4}$ hour, where the front of flow is at 125 mm, is very similar to some of the C^{14} curves obtained by Vernon and Aronoff (1).

4. OSMOTIC PRESSURE FLOW: The "pressure flow" theory of translocation (4) accounts for flow in the sieve tubes by the entrance of water into the translocation system under a high osmotic pressure at the end which supplies sugar, and its elimination under a low osmotic pressure at the end which receives sugar. The turgor pressure at the supplying end of the system must, therefore, be sufficient to, at the least, overcome viscous and other resistances through the length of the translocation column, to cause any required momentum increases of liquid in the pipe, and also to squeeze water out of the column against a small osmotic pressure at the receiving end. Although there are several detailed qualitative treatments of the pressure flow theory from a botanical point of view (4, 6, 7), there is no quantitative physical treatment. An attempt in this direction is made in what follows, with the hope that it may make clearer some of the factors involved in the pressure flow theory and their interaction.

A simple model, shown in figure 3, is considered. The left hand pipe, labelled S, contains an upper region in which sugar is produced by photosynthesis, an intermediate region analogous to the sieve tube column, and a lower consuming region in which sugar is removed by respiration or is transformed to an osmotically less active form. Adjacent to the pipe S and separated from it by a rigid membrane, permeable to water but not sugar, is the pipe Z (analogous to the xylem column), containing water, and connected to a water supply that is assumed to be limitless. The walls of both pipes are rigid.

Sugar produced in the photosynthetic region causes an osmotic influx of water which raises the pressure at the head of the column and causes a flow of sugar solution down the column, with water being squeezed below from pipe S into pipe Z. If the photosynthetic and sugar consuming rates are constant a steady state distribution of sugar concentration, pressure, and velocity of flow will eventually be achieved in pipe S. An approximate mathematical description of the steady

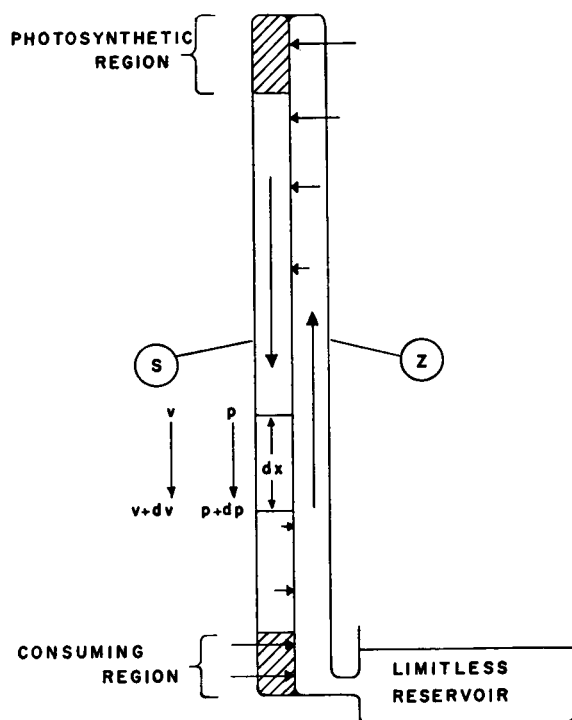


FIG. 3. Simple model for the osmotic pressure flow theory.

state system can perhaps be made in the following way.

The same symbols as were used previously are used here, and the distance x along the pipe is positive in the downward direction. The equation of continuity in pipe S, applicable outside the photosynthetic or consuming regions, states that the number of molecules of sugar passing any pipe cross section is constant, and is written

$$\frac{d(A_p v C_p)}{dx} = 0. \quad (41)$$

If, as in several of the previous models, sugar is removed from solution in the pipe at a rate proportional to its concentration, then this equation is modified to

$$\frac{d(A_p v C_p)}{dx} = -k C_p. \quad (42)$$

In the event that sugar is removed from the pipe at a rate independent of its concentration by an enzyme limited reaction (as, for instance, may occur when the phloem column passes alongside a uniformly active layer of cambium) then the continuity equation becomes

$$\frac{d(A_p v C_p)}{dx} = -\psi, \quad (43)$$

where ψ is a constant.

Since, in the model, the walls of the pipe are rigid and the liquid is incompressible, any passage of water into or out of pipe S must be accompanied by a corre-

sponding passage in the reverse direction somewhere. Therefore, the velocity of flow changes in response to entrance or exit of water. If we make the approximation that the density of sugar solution and water are equal, then the following expression is probably a reasonably good representation of the rate of entrance or exit of water:

$$A_p \frac{dv}{dx} = \alpha C_p - \beta (P_s - P_z), \quad (44)$$

where α and β are constants and P_s is the pressure in pipe S and P_z is the pressure in pipe Z. This says that water enters the pipe at a rate proportional to sugar concentration in the pipe (in analogy to the approximate proportionality between sugar concentration and the equilibrium osmotic pressure) and leaves it at a rate proportional to the pressure difference between pipe S and pipe Z.

The pressure gradients in pipes S or Z can be given, at least approximately, by the following expression

$$\frac{dP}{dx} = -\epsilon v, \quad (45)$$

where P is the pressure in the pipe and ϵ is a constant. The justification for the use of an expression of this type in the present system and the significance of ϵ are discussed in appendix 1.

By the use of any one of the three equations 41, 42, or 43, together with both 44 and 45 (applying to both P_s and P_z), one has the basis for a mathematical description of the system. However, these equations implicitly involve assumptions which are only approximations of greater or lesser reliability. For instance, it is taken for granted in equation 44 that, despite the occurrence of laminar flow, there is good mixing throughout the cross section of the pipe, and the possibility of variation in sieve tube properties along its length is completely ignored. Nevertheless, a further discussion of the model may make some of the features of osmotic pressure flow clearer.

Although it is designed to explain translocation in the phloem, the osmotic pressure flow theory involves a complete cycle of liquid transport down the phloem column and up again through the xylem. The force actuating this cycle is the turgor pressure of the chlorenchyma of the leaf, which, in the simple theory, must be sufficient to do the following: 1) push the flowing liquid through the plasmodesmata, sieve tubes, and sieve plates constituting the translocation column; 2) exert a turgor pressure on the inside of the membranes of the sugar consuming cells sufficiently greater than the equilibrium osmotic pressure of these cells so that water is forced out against the osmotic gradient at a rate necessary to account for the flow rate in the phloem; 3) push an amount of water up through the xylem equal to what has flowed down through the phloem. This last requirement cannot simply be accounted for as part of the ordinary rise of water in the transpiration stream for the osmotic pressure flow theory adds an extra transport burden to the xylem beyond that due to transpiration. One can explain

the extra flow in the xylem as due either to the turgor in the chlorenchyma forcing water through a complete cycle, or to an extra tension in the xylem water column. But these are equivalent since an extra tension in the xylem means that the turgor of the leaf chlorenchyma is correspondingly decreased.

In general one would expect from the simple pressure flow theory that the rate of flow varies with distance along the pipe, according to equation 44. The size of this effect, however, depends on the difference between terms involving concentration in the phloem and pressure. If the pressure dissipation down the pipe is paralleled by a corresponding decline in concentration (as by loss to adjacent tissue), there may be only a small variation in flow rate over long distances.

Crafts (10) has made the interesting suggestion that flow through the sieve plates, under the influence of osmotic pressure, does not occur through the microscopically visible sieve plate perforations, but rather through very small submicroscopic passages. He proposes that these passages have a diameter of about 150 to 450 Å. A quantitative evaluation of this proposal, however, indicates that it makes unacceptably large demands upon the osmotic pressure flow theory. Carman (11) has summarized the physical aspects of water flow through porous media which are used as the theoretical basis for the following calculations.

From measurements on Cucurbita (7), the following are used as reasonable dimensions: 0.05 cm for length of sieve tube element; 3×10^{-5} cm² for cross sectional area; 5×10^{-4} cm for depth of sieve plate. Assume that submicroscopic pores of diameter 4×10^{-6} cm occupy 50% of the cross sectional area of the sieve plate, and an overall velocity of flow of 0.014 cm/sec (50 cm/hr) (3). The velocity of flow through the sieve plate, therefore, is 0.028 cm/sec. One can calculate the pressure drop through one sieve cell and one sieve plate, under these conditions, simply by applying the Hagen-Poiseuille equation (equation 46 in appendix 1). The flow through one sieve cell requires a pressure drop of only about 10^{-5} atmospheres. However, the pressure drop across one sieve plate, where the capillary cross section is about 4×10^{-12} π cm², is one half an atmosphere. Even if the equation for laminar flow between parallel plates (8) is used, the pressure drop across a single sieve plate is still about one fifth or one sixth of an atmosphere. With two sieve plates every millimeter, it would be impossible to expect even an available turgor pressure of 20 atmospheres (10) to cause flow through the translocation column.

5. CYCLOSIS—DIFFUSION TRANSPORT AND ACTIVATED DIFFUSION: Although simple diffusion cannot explain observed rates of translocation (4), it has been suggested (4) that diffusion across cell walls and sieve plates supplemented by rapid mixing within cells, due to cyclosis, might offer an adequate mechanism. Consider the sieve tube column as composed of sieve cells separated from one another by the sieve plates which are permeable to diffusion of the translocate, and suppose that cyclosis within the sieve cells is sufficiently rapid so that there is practically perfect mixing within

each. An estimate of the extent of the increase in transport rate afforded by cyclosis can be obtained by deriving Fick's second law of diffusion (12) for these circumstances.

First, simply consider diffusion across one sieve plate. Distance across the sieve plate is measured along the x axis. According to Fick's first law of diffusion (12), the rate of transfer through a plane of unit area perpendicular to the x axis is approximately

$$F = -D^1 \frac{\Delta C_p}{\Delta x}, \tag{54}$$

where D^1 is the diffusion constant in the sieve plate, ΔC_p is the increase in concentration of translocate across one sieve plate, and Δx is the distance across one sieve plate. When there is a sieve cell adjacent to each sieve plate, equation 54 still expresses the rate of transfer across one sieve plate. However, this rate is also the rate of transfer across one sieve plate plus its adjacent sieve cell, since transfer of translocate across the sieve cell is assumed to be essentially instantaneous. The analogue of Fick's first law for transfer down the column composed of alternate sieve plates and sieve cells, then, is approximately

$$F = -(\omega + 1)D^1 \frac{\Delta C_p}{\Delta x}, \tag{55}$$

where ω is the ratio of the length of the sieve cell to the length of the sieve plate, and Δx is now the distance across one sieve plate plus one sieve cell.

Now the difference between the rate of transfer into and out of an element of the sieve tube column is proportional to the rate of change in concentration in the element. So

$$\Delta F = -\frac{1}{\omega + 1} \left(\frac{\omega}{\eta + 1} + 1 \right) \Delta x \frac{\partial C_p}{\partial t}, \tag{56}$$

where η is the ratio of the volume of the sieve cell that does not contain translocate to the volume that does contain translocate. (Thus, if the sieve cell contained a large inert vacuole and cyclosis only occurred in a thin peripheral layer of cytoplasm, insulated by a membrane from the vacuole, then η would be the ratio of vacuolar to cytoplasmic volume.) Rearrangement of 56 gives

$$\frac{\partial C_p}{\partial t} = -\frac{\omega + 1}{\left(\frac{\omega}{\eta + 1} + 1 \right)} \frac{\Delta F}{\Delta x}. \tag{57}$$

From equation 55 one gets

$$\Delta F = -(\omega + 1)D^1 \frac{\Delta^2 C_p}{\Delta x}, \tag{58}$$

which when substituted in 57 gives

$$\frac{\partial C_p}{\partial t} = \frac{(\omega + 1)^2}{\left(\frac{\omega}{\eta + 1} + 1 \right)} D^1 \frac{\Delta^2 C_p}{(\Delta x)^2}. \tag{59}$$

And if we may pass to the limit, we obtain as the analogue of Fick's second law of diffusion in the sieve tube column,

$$\frac{\partial C_p}{\partial t} = \frac{(\omega + 1)^2}{\left(\frac{\omega}{\eta + 1} + 1\right)} D \frac{\partial^2 C_p}{\partial x^2} \quad (60)$$

If $\eta = \omega - 1$ and if we assume that $\omega = 100$ (7), then the diffusion constant is effectively increased by a factor of about 5,000; if $\eta = 10\omega$, then the diffusion constant is effectively increased by about 9,000 times.³

The mechanism just discussed depends on ordinary diffusion processes subject to Fick's laws (12). However, if use is made of a system that preferentially allows diffusion in one direction, then even further increases in the rate of transfer can be imagined. This might be considered as an expression of the frequently mentioned theory of activated diffusion (13, 14). A theoretical model for such a system has been given (15), but, with it, analyses based simply on Fick's laws are probably no longer valid.

For the model where Fick's laws are applicable, one can make use of well known solutions of the diffusion equation. They will show how closely these models conform to actual data on the distribution of radioactive translocates. If a large amount of a radioactive translocate is applied to a region h surrounding the sieve tube column and it travels down the column by a diffusion mechanism without any of it leaving the column, then we want a solution of the equation

$$\frac{\partial C_p}{\partial t} = D \frac{\partial^2 C_p}{\partial x^2}, \quad (61)$$

subject to the conditions

$$C_p = C_0 \quad x = 0 \quad t > 0 \quad (62)$$

and

$$C_p = 0 \quad x > 0 \quad t = 0 \quad (63)$$

The solution to this problem (12) is

$$\begin{aligned} \frac{C_p}{C_0} &= 1 - \frac{2}{\sqrt{\pi}} \int_0^{\frac{x}{2\sqrt{Dt}}} e^{-\gamma^2} d\gamma \\ &= 1 - \Phi\left(\frac{x}{2\sqrt{Dt}}\right) \end{aligned} \quad (64)$$

where $\Phi\left(\frac{x}{2\sqrt{Dt}}\right)$ is the error function of which extensive tables are available. The kind of distribution given by equation 64 is shown by the curve with the open circles in figure 4. It obviously does not conform to the known data (1, 2, 3).

Another possibility of interest is that, at the same time as the translocate is diffusing down the sieve tube column, it is also leaving the column at a rate

³ An analysis of a similar type may prove of value in helping to understand the movement of growth substances through parenchyma tissue.

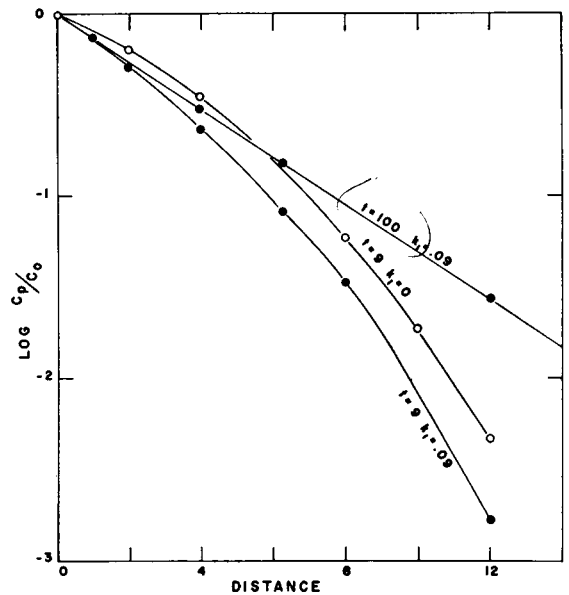


FIG. 4. Distribution of radioactivity with distance and time for two diffusion models. Abscissa is distance along stem in arbitrary units from a constant source of radioactivity. Ordinate is the ratio of concentration of radioactivity in the sieve tube column to that in the constant source in units of logarithm to the base 10. The curve through the open circles is for the model with no loss from the sieve tube column after 9 arbitrary time units. The curves through the closed circles are for the model with loss from the sieve tube column governed by $k_1 = 0.09$ and at 9 and 100 arbitrary time units. The diffusion constant, D , is unity in all cases.

proportional to its concentration in the column. The differential equation in this case becomes (12, p. 124)

$$\frac{\partial C_p}{\partial t} = D \frac{\partial^2 C_p}{\partial x^2} - k_1 C_p \quad (65)$$

with the boundary conditions 62 and 63. Crank (12, p. 130) gives the solution of this problem, and the distributions obtained at two times are shown by the curves through the closed circles in figure 4. With increasing time the curves approach that at $t = 100$ and then do not change. These curves, of course, only account for the radioactivity in the phloem tube and not for that which has been lost irreversibly to the surrounding tissue. Assuming, however, that the shapes of these curves give an approximate representation of the shapes of the curves for total radioactivity (this assumption is certainly valid for longer times), then one can observe some striking similarities between the properties of this model and experimental data (1, 2, 3). At short times the rate of attenuation of radioactivity with distance is greater than it becomes later. At longer times, when C_p approaches its steady state value, the plots of the logarithms of total radioactivity versus distance are straight lines of constant slope and whose ordinate intercepts increase with time. This model, therefore, acts much like the

very first model considered in this paper, of irreversible loss from liquid flowing in a pipe, but at short times probably gives curves departing considerably from a linear relationship between the logarithm of total radioactivity and distance.

6. SURFACE FLOW: A surface active substance accumulating at an interface causes a decrease in the surface tension. If the interface is mobile and only part of it is covered with surface active agent, then there will be a surface pressure difference between the covered and uncovered portion of the interface (equalling the surface tension difference between these parts) and surface flow will occur down the pressure gradient. Van den Honert (16) speculated about this phenomenon as a possible mechanism of translocation and performed some interesting experiments demonstrating transport at a liquid-liquid interface at rates that far exceeded diffusion rates. In order to approach a mathematical analysis of this mode of transport, one can make use of the observations of Crisp (17). He found that the velocity of transport is given by

$$\frac{dx}{dt} = -K_s \frac{\partial \Pi}{\partial x}, \tag{66}$$

where K_s is a constant depending on the properties of the surface active agent, the bulk phases, and the geometry of the system, Π is the surface pressure, and x is distance in the direction of flow. However, the rate of transfer through a line of unit length on the surface and perpendicular to the x axis is

$$F = C_s \frac{dx}{dt}, \tag{67}$$

where C_s is surface concentration of the transported material X . Then, from 66 we get

$$F = -K_s C_s \frac{\partial \Pi}{\partial x}. \tag{68}$$

If we suppose that the substance X behaves on the surface in a manner analogous to an ideal gas (as many surface active substances do under some circumstances (18)), then

$$\Pi = C_s k^1 T, \tag{69}$$

where k^1 is a constant and T is the absolute temperature. Also

$$\frac{\partial \Pi}{\partial x} = k^1 T \frac{\partial C_s}{\partial x}, \tag{70}$$

and upon substituting 70 in 68 we obtain an expression like Fick's first law of diffusion for the case where the diffusion constant is proportional to concentration:

$$F = -k^1 T K_s C_s \frac{\partial C_s}{\partial x}. \tag{71}$$

An analogue of Fick's second law (equation 61) is, then,

$$\frac{\partial C_s}{\partial t} = -\frac{\partial F}{\partial x} = k^1 T K_s \left\{ \left(\frac{\partial C_s}{\partial x} \right)^2 + C_s \frac{\partial^2 C_s}{\partial x^2} \right\}. \tag{72}$$

For the problem of transport in the phloem, this equation might apply under similar conditions as equation 61, where there is no loss from the phloem column to surrounding tissue. If substance X is lost to surrounding tissue irreversibly, however, then the following modification (analogous to equation 65) might apply:

$$\frac{\partial C_s}{\partial t} = k^1 T K_s \left\{ \left(\frac{\partial C_s}{\partial x} \right)^2 + C_s \frac{\partial^2 C_s}{\partial x^2} \right\} - k^{11} C_s. \tag{73}$$

The steady state solution of equation 65, describing diffusion down the sieve tube column at the same time as translocate is being lost irreversibly to the surrounding tissue, gives a result according well with experimental observations (2, 3). It is, therefore, of interest to see how well the steady state modification of 73, the analogous equation for surface flow, conforms to these data. An equation more amenable to analysis than 73 is obtained in appendix 2 and is

$$\frac{dC_s}{dx} = -\sqrt{\frac{2k^{11}C_s}{3k^1 T K_s} + \frac{c_1}{C_s^2}}, \tag{79}$$

where c_1 is a constant determined by the boundary conditions. However, the experimental data generally show a relationship between radioactivity and distance that can be described approximately by the relationship

$$\frac{dC}{dx} = -aC, \tag{80}$$

where C is radioactivity per unit length and a is a constant. This is quite different from 79, and, therefore, the simple model using surface flow does not appear to be a useful one for explaining translocation data.

DISCUSSION

The characteristics of three main categories of mechanisms have been considered in this paper. They are 1), translocation by a continuous "en masse" flow through the length of the phloem column as is discussed in models 1, 2, 3, and 4; 2), cyclosis-diffusion transport discussed in model 5; and 3), surface flow as discussed in model 6. Under the assumption that translocate is absorbed irreversibly from the phloem column at a rate proportional to its concentration therein, one can nicely reproduce many important features of the experimental data by the use of flow type models and the cyclosis-diffusion model. The surface flow model is not so successful in this respect.

The valid use of a mathematical model is to help organize and interpret experimental data and to perhaps help direct the course of further investigation. Good quantitative data on translocation is relatively scarce and the models presented here are, therefore, not subject to comparison with a sufficiently broad range of experimental data to allow them to be accepted or rejected. Although the characteristics of much of the experimental data with radioisotopes can be reproduced by some of the models, there can arise

serious doubts about the "actuality" of the models studied. The mathematical analysis of models frequently involves gross simplification of the biological facts, and the types of models considered may be dictated largely by their simplicity and the mathematical skill of the author. In the present paper there are numerous simplifications and approximations, and a number of plausible models have not even been considered. For instance, the analysis of bidirectional flow within a single phloem strand was abandoned because of mathematical difficulties, and the cyclosis-diffusion model with a time variable source has not been presented.

It is possible to distinguish at least two markedly different possible mechanisms actuating "en masse" flow through the length of the phloem column (4). These are a) flow, such as that in osmotic pressure flow, and b) flow, like the flow in cytoplasmic streaming, that is actuated by the living protoplasm. Some possible modes of experimentally distinguishing the two may lie in these differences:

1) Pressure flow demands that there be a hydrostatic pressure gradient down the phloem column, while streaming flow does not require such a gradient.

2) In general, one would expect a flow velocity gradient along the phloem column in an osmotic pressure flow system, while streaming flow does not require this.

3) Osmotic pressure flow demands that there be a circulation of water in the xylem complementary to that in the phloem, while circulation by cytoplasmic streaming could occur completely in one phloem strand or from strand to strand. Clements (14) has criticized the osmotic pressure flow theory because of his failure to observe sufficient water movement in the xylem, though Crafts (9) believes these arguments have been adequately answered.

4) Streaming flow is dependent on a metabolic energy source, and, therefore, one might expect it to be more susceptible than pressure flow to interference with metabolism. However, pressure flow is dependent on the maintenance of a semi-permeable membrane, and this may also be dependent on normal metabolic activity. (In addition, it is possible that the pressure developed in a plant cell may be, at least in part, due to an active metabolic process (19, 20).)

5) Osmotic pressure flow precludes two way flow within a single phloem strand and perhaps also even within the stem taken as a whole. There is no such limitation with streaming flow.

6) Streaming flow demands that streaming occur in the phloem and apparently this has never been unequivocally observed (9, 21).

7) Streaming is known to be a phenomenon sensitive to even slight disturbances such as mechanical shocks, while pressure flow should be more resistant.

SUMMARY

A number of models to explain the short term translocation patterns of isotopically labeled materials are analyzed mathematically:

1. "En masse" flow of translocate solution through a pipe with irreversible loss of translocate to the surrounding tissue.

2. Like model 1, except translocate is lost reversibly.

3. Like model 1, but the approach to the steady state in the region of isotope application is considered.

4. Osmotic pressure flow model.

5. Cyclosis-diffusion model.

6. Surface flow model.

Models 1 and 3 predict distributions of isotope that conform well with certain experimental results. Models 2 and 6 do not seem so successful in this respect. Model 4 is the most difficult to analyze, but the results indicate that, in general, one should expect both a velocity gradient and a hydrostatic pressure gradient along the translocation column. Analysis of model 5 indicates how much one may expect cyclosis to speed up the transport of solutes, and the predicted distributions of isotope from this model are close to certain experimental results; a possible contribution of an "activated diffusion" to this model is also mentioned.

APPENDIX 1, *Derivation of an Expression for the Pressure Gradient for the Pressure Flow Theory*: A number of writers (7, 9) on the pressure flow theory have made quantitative or qualitative use of the Hagen-Poiseuille equation to express the pressure gradient in the translocation pipe:

$$\frac{dP}{dx} = - \frac{8\pi\mu v}{A_p} \quad (46)$$

where μ is the viscosity of the flowing liquid. This equation is strictly applicable only in the case of laminar, non-accelerated flow in a circular tube of uniform cross section. Some justification, therefore, ought to be offered for its application to the sieve tube column where there is frequent interference to flow by the sieve plates and where, according to equation 44, there is acceleration of the flow due to entrance or exit of water through the pipe walls. In what follows the particular form of equation 46 is discarded, but it is concluded, nevertheless, that the pressure gradient can be reasonably accurately represented by an equation of the form

$$\frac{dP}{dx} = - \epsilon v, \quad (45)$$

where ϵ is a constant.

In order to obtain an estimate of the magnitude of the Reynold's number for flow of a 10 % sucrose solution through the sieve tube column, use was made of sieve tube dimensions given by Crafts (7) for *Cucurbita* and translocation velocities given by Biddulph and Cory (3). Using 1.04 grams/cm³ for density, 0.014 cm/sec (50 cm/hr) for velocity, 0.0050 cm for diameter, and 0.015 poise for viscosity gives a value of 4.8×10^{-3} for the Reynold's number in flow through the sieve tube lumen, and using 0.35 cm/sec for velocity and 0.00015 cm for diameter gives a Reynold's number of 3.6×10^{-3} for flow through the sieve plate

pores, assuming they are open and available for flow. These values are very far below the lower critical Reynold's number (8) and, therefore, flow in the sieve tube column is certainly laminar.

As a matter of fact these Reynold's numbers are so small that effects of viscosity should far outweigh accelerative effects. Experimental data given by Rouse (8, figures 85 and 129) indicate that at such low Reynold's numbers, the Euler number, determining the characteristics of flow under specific boundary conditions, is proportional to the square root of the Reynold's number. From the definition of the Euler and Reynold's numbers, therefore, one can deduce that even when the sieve tube pipe undergoes marked changes in form, as at the sieve plate, the dissipation of pressure is still proportional to the first power of the average flow velocity.

The contribution of the inertial effects, due to entrance or exit of water through the pipe walls, to the pressure gradient can, as a first approximation, be estimated by deriving a modified Bernoulli equation. First note, referring to figure 3, that gravitational force need not be a consideration since the flow is essentially no more than an eddy within a liquid, of uniform density, which is stationary as a whole. The distance, x , along the pipe S is positive downwards. The force acting on the element dx due to the pressure gradient is $-A_p dP$. From the considerations of the preceding paragraph, the viscous resistance is $-A_p \epsilon v dx$, where ϵ is a constant proportional to viscosity and v is the average rate of flow.

The momentum changes occurring in the element dx are due to acceleration from v to $v + dv$ of liquid entering dx from the adjoining element above it, and also to acceleration from zero to $v + dv$ of liquid entering dx by diffusion through the pipe walls. Since, for constant cross sectional area, the increase in velocity, dv , can be attributed entirely to influx of water through the walls, that fraction of the total liquid leaving dx which entered dx from the adjoining segment is $v/(v + dv)$. Therefore, the mass of water leaving dx in time dt which had to be accelerated from v to $v + dv$ is

$$\frac{v}{v + dv} \rho A_p (v + dv) dt = v \rho A_p dt, \quad (47)$$

and the force necessary for the required acceleration is

$$v \rho A_p dt \frac{dv}{dt} = \rho A_p v dv, \quad (48)$$

where ρ is the density of the liquid.

The other part of the liquid leaving dx has a mass

$$\frac{dv}{v + dv} \rho A_p (v + dv) dt = dv \rho A_p dt \quad (49)$$

and the rate at which mass is added to the flowing liquid is, therefore,

$$\frac{dm}{dt} = \rho A_p dv. \quad (50)$$

The force necessary to cause the corresponding rate of change of momentum is

$$v \frac{dm}{dt} = \rho A_p v dv. \quad (51)$$

The relation between the four forces considered is the modified Bernoulli equation:

$$-A_p dP - A_p \epsilon v dx = 2 \rho A_p v dv \quad (52)$$

or

$$\frac{dP}{dx} = -\epsilon v - 2 \rho v \frac{dv}{dx}. \quad (53)$$

However, if one approximates the viscous resistance term on the right hand side by using the Hagen-Poiseuille equation and compares it to values of the second term calculated from known rates of translocation (3), then it is seen that only the viscous resistance term is important. Therefore, equation 45 should be a reasonable representation of the pressure gradient.

APPENDIX 2, *A Simplification of the Steady State Modification of Equation 73*: Equation 73, in the steady state, becomes

$$k^1 TK_s C_s \frac{d^2 C_s}{dx^2} + k^1 TK_s \left(\frac{dC_s}{dx} \right)^2 - k^{11} C_s = 0 \quad (74)$$

If we let $\eta = \frac{dC_s}{dx}$, then $\frac{d^2 C_s}{dx^2} = \frac{d\eta}{dx} = \eta \frac{d\eta}{dC_s}$ and equation 74 can be put in the form

$$k^1 TK_s C_s \eta \frac{d\eta}{dC_s} + k^1 TK_s \eta^2 = k^{11} C_s, \quad (75)$$

or

$$k^1 TK_s C_s \frac{d(\eta^2)}{dC_s} + 2k^1 TK_s \eta^2 = 2k^{11} C_s. \quad (76)$$

Multiply through by $C_s dC_s / k^1 TK_s$ and get

$$C_s^2 d(\eta^2) + 2C_s \eta^2 dC_s = \frac{2k^{11}}{k^1 TK_s} C_s^2 dC_s \quad (77)$$

or

$$d(\eta^2 C_s^2) = \frac{2k^{11}}{k^1 TK_s} C_s^2 dC_s. \quad (78)$$

Integration of 78 then gives as the acceptable result

$$\frac{dC_s}{dx} = -\sqrt{\frac{2k^{11} C_s}{3k^1 TK_s} + \frac{c_1}{C_s^2}}, \quad (79)$$

where c_1 is the integration constant.

SYMBOLS USED

- h**: The distance along which the source region h , containing the reservoir of applied radioactive material, extends adjacent to the phloem tube.
- C₁**: The concentration of radioactive tracer in region h .
- X**: The name of the radioactive material.

- K: The first order constant characterizing the rate of transfer of X from the region h into the phloem tube.
- v: The velocity of flow of fluid in the phloem tube.
- C₀: The concentration of X in the phloem tube at the outflowing edge of region h (at x = 0).
- A_p: The cross sectional area of the phloem tube.
- x: Distance along the pipe measured from the outflowing edge of region h and going in the positive direction away from region h.
- t: Time.
- C_p: Concentration of X in phloem tube at any distance x.
- C_t: Concentration of X in the tissue surrounding the phloem tube at any distance x.
- k: The first order constant characterizing the rate of loss of X from the phloem tube to the surrounding tissue.
- A_t: The cross sectional area of the tissue surrounding the phloem tube.
- k₁: k/A_p.
- k₂: k/A_t.
- e: Base of natural logarithm.
- σ: Rate of photochemical fixation of CO₂ in the region h.
- λ: Isotopic ratio of C¹⁴O₂.
- A_h: Average cross sectional area of the region h.
- K₁: K/A_p.
- v: Rate of loss of X from region h into the phloem tube.
- v_c: v/hA_h.
- A: A_p/hA_h.
- γ: $A v \left(1 - e^{-\frac{K_1 h}{v}} \right)$, is the time constant describing the approach to the steady state concentration of X in the region h.
- ψ: A zero order rate constant for loss of X from the phloem pipe.
- α: Proportionality constant between rate of osmotic flow of water and concentration difference across the semi-permeable membrane.
- β: Proportionality constant between rate of flow of water through the semi-permeable membrane and hydrostatic pressure difference across the membrane.
- P: Hydrostatic pressure in the xylem or phloem.
- P_s: Hydrostatic pressure in pipe S (analogous to the phloem) in the osmotic pressure flow model.
- P_z: Hydrostatic pressure in pipe Z (analogous to the xylem) in the osmotic pressure flow model.
- ε: A constant, proportional to viscosity, that describes the relationship between the hydrostatic pressure gradient and velocity of flow.
- π: Proportionality constant between circumference and diameter of a circle.
- μ: Viscosity.
- ρ: Density of liquid flowing in the xylem or phloem.
- m: Mass.
- D¹: Ordinary diffusion constant.
- F: Diffusion or surface flow flux.
- ω: Ratio of sieve cell length to sieve plate length.
- γ: Ratio of vacuolar volume to cytoplasmic volume in the sieve cell.
- D: Diffusion constant in the cyclosis-diffusion model.
- K_s: Proportionality constant between surface flow velocity and surface pressure gradient.
- Π: Surface pressure.
- C_s: Surface concentration at any distance x.
- k¹: Proportionality constant relating surface pressure, concentration, and temperature.
- T: Absolute temperature.
- k¹²: The first order constant characterizing the rate of loss of X from the phloem tube to the surrounding tissue in the surface flow model.

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LITERATURE CITED

1. VERNON, L. P. and ARONOFF, S. Metabolism of soybean leaves. IV. Translocation from soybean leaves. *Arch. Biochem. Biophys.* 36: 383-398. 1952.
2. SWANSON, C. A. and WHITNEY, J. B., JR. Studies on the translocation of foliar-applied P³² and other radioisotopes in bean plants. *Amer. Jour. Bot.* 40: 816-823. 1953.
3. BIDDULPH, O. and CORY, R. An analysis of translocation in the phloem of the bean plant using THO, P³², and C¹⁴O₂. *Plant Physiol.* 32: 608-619. 1957.
4. CURTIS, O. F. *The Translocation of Solutes in Plants.* McGraw-Hill, New York 1935.
5. SCHUMANN, T. E. W. Heat transfer: A liquid flowing through a porous prism. *Jour. Franklin Inst.* 208: 405-416. 1929.
6. MÜNCH, E. Versuche über den Saftkreislauf. *Ber. deutsch. bot. Ges.* 45: 340-356. 1927.
7. CRAFTS, A. S. Movement of organic materials in plants. *Plant Physiol.* 6: 1-41. 1931.
8. ROUSE, H. *Elementary Mechanics of Fluids.* Wiley, New York 1946.
9. CRAFTS, A. S. Movement of assimilates, viruses, growth regulators, and chemical indicators in plants. *Bot. Rev.* 17: 203-284. 1951.
10. CRAFTS, A. S. Movement of materials in phloem as influenced by the porous nature of the tissues. *Discussions Faraday Soc.* 3: 153-159. 1948.
11. CARMAN, P. C. Some physical aspects of water flow in porous media. *Discussions Faraday Soc.* 3: 72-77. 1948.
12. CRANK, J. *The Mathematics of Diffusion.* Oxford University Press, Oxford 1956.
13. MASON, T. G. and PHILLIS, E. The migration of solutes. *Bot. Rev.* 3: 47-71. 1937.
14. CLEMENTS, H. F. Movement of organic solutes in the sausage tree, *Kigelia Africana*. *Plant Physiol.* 15: 689-700. 1940.
15. FRANCK, J. and MAYER, J. E. An osmotic diffusion pump. *Arch. Biochem.* 14: 297-313. 1947.
16. VAN DEN HONERT, J. H. On the mechanism of transport of organic materials in plants. *Proc. Koninkl.*

- Akad. Wetenschap. Amsterdam 35: 1104-1111. 1932.
17. CRISP, D. J. Two-dimensional transport at fluid interfaces. *Trans. Faraday Soc.* 42: 619-635. 1946.
18. HARKINS, W. D. Intermolecular forces and two dimensional systems. *Surface Chemistry, Publication no. 21, AAAS* 1943.
19. SPANNER, D. C. The active transport of water under temperature gradients. *Symposia Soc. Exptl. Biol.* VIII: 76-93. 1954.
20. BENNET-CLARK, T. A. Non-osmotic water movement in plant cells. *Discussions Faraday Soc.* 3: 134-139. 1948.
21. CURRIER, H. B., ESAU, K. and CHEADLE, V. I. Plasmolytic studies of phloem. *Amer. Jour. Bot.* 42: 68-81. 1955.

EFFECTS OF INDOLEACETIC ACID ON THE UTILIZATION OF ACETATE-1-C¹⁴ BY PEA STEM SLICES¹

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Studies on the utilization and evolution of acetaldehyde by plant tissues suggest that indoleacetic acid (IAA) may influence the partition of pyruvate and related products of glycolysis into various metabolic pathways (5, 6). Boroughs and Bonner (1) tested this possibility in their study of the effects of IAA on the metabolism of acetate-1-C¹⁴ by *Avena coleoptiles*. Except for a very appreciable stimulation of incorporation of activity into the non-cellulosic polysaccharides by IAA, they found no notable response to the auxin. It was demonstrated later that in wheat roots IAA significantly affects incorporation of activity from C¹⁴-labeled pyruvate and acetate into organic acids, sugars, polyuronide hemicelluloses, pectic substances, lipides and cellulose (7, 8). Studies by Perlis (9), however, on the utilization of acetate-1-C¹⁴ by pea stem slices revealed experimental effects of doubtful significance.

Recent work in this laboratory indicates that effects of IAA on the metabolism of acetate by pea stem tissue can be demonstrated conclusively in experiments involving pre-treatment of the slices with IAA followed by brief exposure to the labeled substrate (4). Experiments of this sort are described below.

MATERIALS AND METHODS

Pea seedlings (var. Alaska) were grown in the dark at 20° C on sphagnum saturated with 0.025 M CaCl₂ and were used for the experiments 8 days after the seeds were planted. Preliminary experiments had shown that stem sections from peas grown in this manner exhibit a more impressive growth response to IAA than those from seedlings given a more complex nutrient solution. Transverse slices, 2 mm in length, were cut from a section of the stem extending from about 2 to 12 mm below the epicotyl arch. The slices were washed, then centrifuged in a perforated container at a low speed to remove adhering water.

Acetate-1-C¹⁴ having a specific activity of 6.7 millicurie/millimole was the source of carbon 14. This material was available as the potassium salt and was used in this form for most of the experiments. For

use in two experiments the salt was converted to the calcium salt by passing a solution of it through a column containing the calcium form of Duolite C-3. Most of the experiments of this study involve a pre-treatment period during which the stem tissues were incubated in various non-radioactive solutions. For pre-treatment the solutions and tissues were placed in Erlenmeyer flasks of one liter capacity and these were placed on a shaker to effect aeration of the solution. During the period of exposure to radioactive acetate the slices and solutions were in closed containers (Pyrex gas washing bottles, no. 31760). A short piece of capillary tubing replaced the fritted glass aerator usually found in this assembly. The outlet tube was attached to the inlet tube of a second gas washing bottle. This bottle, containing 0.1 N NaOH to trap CO₂, was equipped with a fritted glass aerator. Carbon dioxide-free air was supplied for the aeration of the slices. Fresh weights of tissues used in the experiments ranged from 3.25 to 7.0 g.

After exposure to radioactive acetate the washed slices were extracted with boiling, 95 % ethanol and then with an equal volume of boiling, 70 % ethanol. Three extractions with each solvent mixture were made and a total volume of 250 ml of extractant was used for each sample. This is the 1st step of a fractionation procedure which is outlined in figures 1 and 2.

Fractionation of the ethanol extract (fig 1) involved removal of the ethanol, after the solution was adjusted to pH 9.0 with NaOH, by vacuum distillation, acidification and extraction of the aqueous residue with ether for 72 hours by a method essentially that described by Isaacs and Broyer (2) and separation of the lipides from the organic acids in the ether extract by addition of water and titration of the acids with NaOH to pH 8.5. The ethereal solutions were dried down on a warm water bath and the residue taken up in chloroform. Activity in the chloroform solution was determined by the technique of direct plating, as were all other determinations of activity reported here. Details of the counting procedure are given below. The aqueous solution from the ether extract was brought to dryness on a hot water

¹ Received August 6, 1957.