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A Simple Theory Regarding Ambimobility of Xenobiotics with Special Reference to the Nematicide, Oxamyl

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ABSTRACT

A theory is presented to explain the phloem mobility of certain systemic xenobiotics that are not weak acids. It is shown that there is a theoretically optimum permeability that permits optimum circulation through the symplasm and apoplast (including the phloem and xylem) of *Solanum tuberosum* plants. The optimum permeability is large enough to permit substantial passive permeation into sieve cells in the source leaf and yet is small enough to permit phloem transport with some retention. The optimum permeability is a function of the velocity of sap flow in sieve tubes, the radius of the sieve tube, the over-all length of the plant, and the length of the carbohydrate and xenobiotic sources. It is argued that the nematicide, oxamyl, is near the optimum permeability under some experimental conditions. It is shown that depending on the strength of the carbohydrate sink in roots or growth points and depending on the permeability of the xenobiotic, there can be passive accumulation of xenobiotics in the sieve tubes in the carbohydrate sink regions.

The patterns of translocation which various xenobiotic substances display after entering a plant have been described for many chemicals, especially herbicides (1). Two distinctive patterns of transport were discerned, namely the apoplastic pattern and the symplasmic pattern. Movement in the apoplast occurs mainly via the xylem and the cell walls of the parenchyma cells, while movement in the symplasm occurs via the phloem and the interconnected protoplasts of the parenchyma cells. Chemicals moving by both routes are called ambimobile (5). It has been assumed that the potential for a chemical to penetrate the plasmalemma of the cells is correlated with the over-all pattern of translocation it achieves in the plant as a whole. It was originally thought that chemicals displaying an apoplastic transport pattern were unable to penetrate the plasmalemma of plant cells and thus were excluded from the plant symplasm but recent investigations have shown that several chemicals termed apoplastic do penetrate plant cell membranes (4, 7–10, 13). Peterson and Edgington (7) have called such chemicals pseudoapoplastic. They suggested that the permeability of the plasmalemma to the pseudoapoplastic chemical is so great that it cannot be retained in the symplasm for long without being leached into the apoplast and carried away with the transpiration stream.

In some cases it is desirable to have an ambimobile xenobiotic chemical which would be distributed widely throughout a plant after a foliar spray. The chemical would travel down to the roots in the phloem and continuously circulate back again in the xylem so that even the leaves and roots formed after the spray treatment would be protected.

There are at least two ways that a xenobiotic can become phloem mobile that do not involve special carrier molecules located in the membrane. One idea, known as the weak acid hypothesis, had been described by Crisp (3). According to this theory, weak acids which are in the undissociated molecular state at low pH are able to diffuse through the plasmalemma due to their lipid solubility. Once inside the plasmalemma, the higher pH of the cytoplasm causes the molecules to dissociate and the polar anions are unable to diffuse back through the plasmalemma. In this way a weak acid xenobiotic can be loaded into the phloem and transported away.

There is some evidence (6) that the nematicide oxamyl is ambimobile by virtue of having an intermediate permeability. The uptake of oxamyl by parenchymatous tissue of potato tuber appears to be passive because: (*a*) oxamyl is not concentrated within the cell; (*b*) it is free to diffuse out when the tissue is transferred to oxamyl-free medium; and (*c*) the tested effects of temperature, oxamyl concentration, and a respiratory inhibitor all indicated passive uptake. Also, oxamyl is reasonably stable, not degrading substantially to other chemical forms until 9 days have elapsed in these experiments. Thus, oxamyl displayed an ambimobile transport pattern in potato plants (2, 6) but was not actively taken up by the parenchyma cells (6). Penetration into the cells occurred more slowly than was the case for the pseudoapoplastic chemicals studied previously (7). Oxamyl does not show active vein loading (Pinkas and Edgington, unpublished data).

According to what could be termed the intermediate permeability hypothesis, the chemical will diffuse passively into the symplasm of the phloem and will be carried away along with the assimilates. The permeability of the chemical is such that it is retained within the sieve tube long enough to be transported to carbohydrate sinks. As symplasmic transport occurs, the chemical continuously leaks out of the symplasm into the apoplast and thus displays ambimobile translocation.

Here, we examine the question of rate of membrane penetration of stable xenobiotics and their transport pattern in the plant on a theoretical level and to see if the known permeabilities to oxamyl and the pseudoapoplastic chemicals can account for their observed patterns of transport in the plant.

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MATERIALS AND METHODS

The method of determining the permeability of parenchymatous cells of potato tubers (*Solanum tuberosum*) to oxamyl and other xenobiotics has been described previously (7). In summary, discs 1 mm in thickness were cut from cores 1 cm in diameter taken from the internal phloem region of a potato tuber. The discs were rinsed with running tap water for 20 min, gently blotted, and 1.3 g of tissue was placed into a vial containing 3.5 ml of a solution 2×10^{-5} M in [^{14}C]oxamyl (1.23 mCi/mmol), 10^{-4} M in $CaSO_4$, and 0.05 M in citrate-phosphate buffer (pH 5.3). The volume of the ambient solution was small so that a measurable amount of oxamyl would disappear from the ambient solution as the oxamyl diffused into the tissue. At intervals of 0, 15, 30, 60, 120, 180, 240, and 300 min from the time of addition of the tissue, 50-μl samples were removed from the ambient solution and the amount of oxamyl in the sample was determined by counting. The experiment was repeated three times, with four replicates in each experiment. It was shown previously (6) that oxamyl is not broken down metabolically by the potato tuber tissue during the experimental time, nor is oxamyl volatile. The amount of oxamyl lost from the ambient solution equals the amount entering the tissue.

Dry weight determinations were made on three samples of discs prepared as described above. The weight remaining after heating at 60 C to constant weight was taken as the dry weight of the tissue.

In order to measure sieve tube diameters in the potato plant, longitudinal sections of stems were cut by hand. Sections were stained for callose with 0.01% aniline blue in 0.05 M phosphate buffer (pH 7.5) and observed with a Nikon epifluorescence microscope to locate the sieve tubes. Diameters of 24 sieve tubes were measured. To determine the diameters of cells in the potato tuber tissue, measurements of 24 cells were made from free hand sections of the tissue.

THEORY

We will presume that the xenobiotic is biochemically stable and that it passively moves across the plant cell membranes. (Oxamyl appears to meet these criteria.) Once the xenobiotic has been taken up into the leaf apoplast the passive leakage into the sieve tubes will allow it to be carried away with the photosynthate. After the xenobiotic moves out of the source zone in the phloem some will slowly leak out and be swept up again in the xylem stream while the rest will contribute to an over-all increase in xenobiotic concentration downstream. If the volume flow rates of phloem translocation and of xylem transpiration remained constant, then the plant would tend toward a steady-state with respect to xenobiotic distribution. The xenobiotic concentration beyond the sink would build up to a constant stable value because then the rate of leakage out of the phloem to the xylem stream would exactly equal the rate of phloem bound transport of the xenobiotic.

In practice a steady-state never would be obtained in a plant because the volume flow rate of sap movement through the xylem and phloem would vary diurnally and independently of each other. Because of the complexity of the vascular system in a real plant and because of the large number of independent factors determining sap flow velocities, it would never be practical to derive an exact model giving the spacial and temporal distribution of a xenobiotic in a plant. It would be valuable to derive a steady-state model for a linear (unbranched) vascular system in which daily average figures are used for xylem and phloem transport rates.

The basic attributes of our model are illustrated in Figure 1. The vascular system, represented by a single xylem vessel and a single sieve tube, runs the total length of a "linearized" plant consisting of a leaf blade of length L (in units of meters, m). The over-all length of the plant is L(m) and the stem petiole and leaf blade combined are 0.5L m long. The sap velocity, V (m sec^{-1}), in the leaf blade increases linearly with distance until it reaches a maximum value of V (m sec^{-1}) in the petiole and stem. In the root the sap velocity again decreases linearly with distance until it nearly reaches zero. This pattern of sap velocity changes is consistent with a Münch pressure-flow translocation model of short path length (11). But even if the Münch model is wrong the same velocity pattern would exist as long as water entered the source zone phloem at a uniform rate over the membrane surface and if water exited from the sink phloem uniformly. The xenobiotic is presumed to be in the apoplast at a uniform concentration C° mol m^{-3}, in the leaf zone over a distance l* which may be less than or equal to l, *i.e.* the xenobiotic may or may not be confined to the leaf margins. Beyond the xenobiotic source, the apoplastic (including the xylem) concentration is presumed small compared to the adjacent phloem concentration. This is likely to be true in a steady-state because at any point along the path the mol sec^{-1} of xenobiotic moving up the xylem must equal the mol sec^{-1} moving down the phloem. The concentration times volume flow rate equals the transport rate in mol sec^{-1}. If the xylem volume flow rate is V_x (m^{3}sec^{-1}) and the phloem volume flow rate is V_p and the corresponding concentrations are C_x and C_p, then $V_xC_x = V_pC_p$ and $C_x/C_p = V_p/V_x$. Since V_x is likely to be much larger than V_p, C_x is also small compared to C_p.

THE GOVERNING DIFFERENTIAL EQUATION

The governing differential equation for this problem is derived

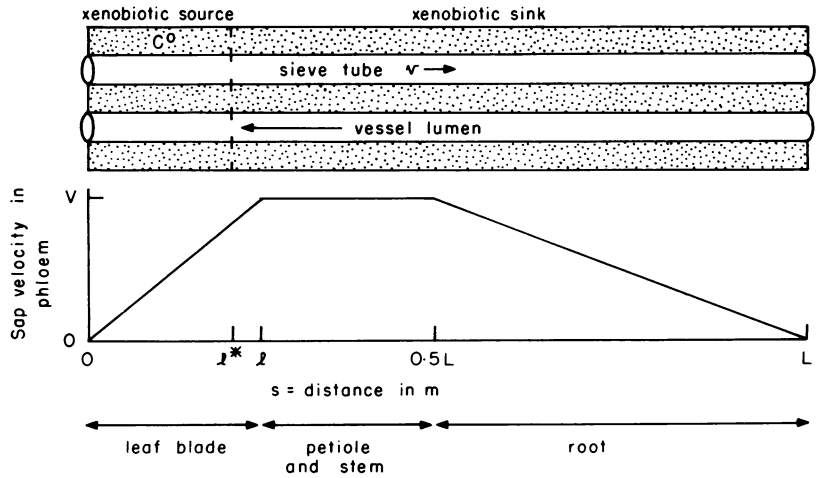

FIG. 1. Diagram showing model system. See text for description. Stippled area represents apoplast outside xylem vessel lumen.

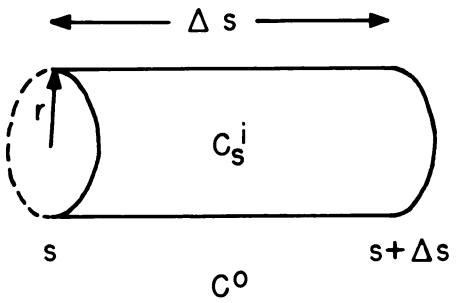

FIG. 2. Short length, Δs, of sieve tube of radius r. Xenobiotic is at concentration C_s^i inside and C° outside.

by considering a short length, Δs, of sieve tube (as in Fig. 2). In the steady-state, the factors contributing to the movement of the xenobiotic through the ends and the membrane must sum up to zero so that C^i, the internal concentration, does not change with time. The equation that satisfies the conditions is[2]

$$\frac{2}{r}P^*(C_s^i - C^\circ) + v_s\frac{dC_s^i}{ds} + C_s^i\frac{dv_s}{ds} = 0 \qquad (1)$$

Equation 1 ignores the contribution of diffusion to transport down sieve tubes, but this is justifiable except when V_s is very nearly zero a few hundred μm from the leaf tip or root apex (12). If a large fraction of the xenobiotic enters the sieve tubes by way of plasmodesmata in common with adjacent cells, and if said transport is limited by the membranes of sieve tubes and adjacent cells, then equation 1 would require a minor modification; the first term would then contain a coefficient α equal to the ratio of the total membrane surface area for penetration into the phloem to the sieve tube membrane surface area. The reader wishing to take this modification into account need only substitute P* with αP* in all subsequent equations.

SOLUTIONS OF THE DIFFERENTIAL EQUATION (1)

Our aim is to solve equation 1 to determine the concentration of the xenobiotic in the root phloem as a fraction of C°, the concentration in the source apoplast.

In the Leaf. The sap velocity in the source leaf sieve tube can not be allowed to start at zero, otherwise the solution of equation 1 leads to an improper integral. The velocity, V, will increase linearly if water enters uniformly over the sieve tube membrane including the circular end of the cylinder. If J* is the membrane water flux then $V = J^*(\pi r^2 + 2\pi rl)$ and $v_s = J^*(\pi r^2 + 2\pi rs)$ from which

$$v_s = V\left(\frac{2s+r}{2l}\right) \qquad (2)$$

and

$$\frac{dv_s}{ds} = \frac{V}{l} \qquad (3)$$

also in the source leaf C° is constant and nonzero by hypothesis for $0 \leq s \leq l^*$. Substituting equations 2 and 3 into 1 we get

$$\frac{2}{r}P^*(C_s^i - C^\circ) + \frac{V}{l}C_s^i + V\left(\frac{2s+r}{2l}\right)\frac{dC_s^i}{ds} = 0 \qquad (4)$$

We can rearrange equation 4 and integrate it from $C_s^i = 0$ to $C_{l^*}^i$ and $s = 0$ to l^*. This gives

$$C_{l^*}^i/C^\circ = \frac{P^*}{P^* + \frac{Vr}{2l}}\left[1 - \exp\left(-\left[\frac{2lP^*}{rV} + 1\right]\ln\frac{2l^*+r}{r}\right)\right] \qquad (5)$$

Had v_s been a constant equal to V a much simpler answer would have emerged.

$$C_{l^*}^i/C^\circ = 1 - \exp\left(\frac{-2P^*}{rV}l^*\right) \qquad (6)$$

[2] For a full derivation, write to M. T. Tyree at the Istituto di Botanica.

If the length of the xenobiotic source, l*, is less than the length of the leaf, l, then we must solve equation 1 with C° = 0 for $l^* \leq s \leq l$ and the conditions in equations 2 and 3. This gives

$$C_l^i/C_{l^*}^i = \exp\left[-\left(\frac{2lP^*}{rV} + 1\right)\ln\frac{2l+r}{2l^*+r}\right] \qquad (7)$$

In the Stem. By hypothesis v_s is a constant maximum equal to V and C° = 0 for $l \leq s \leq 0.5L$ in the stem. So dv_s/ds in equation 1 is zero. We can rearrange equation 1 and integrate from $C_s^i = C_l^i$ to $C_{0.5L}^i$ and from s = l to 0.5L. This gives

$$\frac{C_{0.5L}^i}{C_l^i} = \exp\left(-\frac{2P^*}{rV}(0.5L - l)\right) \qquad (8)$$

In the Root. The sap velocity is declining in the root and again v_s cannot equal zero at s = L. So

$$v_s = V\left(1 - \frac{s-0.5L}{L-0.5L} + \frac{r}{2(L-0.5L)}\right) \qquad (9)$$

and

$$\frac{dv_s}{ds} = -\frac{2V}{L} \qquad (10)$$

Substituting equations 9 and 10 into 1 and setting C° = 0 in the root we can integrate the equation. Since the diffusion term is ignored in equation 1 it is best to integrate only part way to the root tip, *e.g.* s = 0.9L. This yields

$$\frac{C_{0.9L}^i}{C_{0.5L}^i} = \exp\left[+\left(\frac{LP^*}{rV} - 1\right)\ln\frac{0.2L+r}{L+r}\right] \qquad (11)$$

The parameter we wish to solve for is the ratio of xenobiotic concentration at $s = 0.9L = C_{0.9L}^i$ to C°. This can be computed from the product of equations 5, 7, 8, and 11 because

$$\frac{C_{0.9L}^i}{C^\circ} = \frac{C_{0.9L}^i}{C_{0.5L}^i}\frac{C_{0.5L}^i}{C_l^i}\frac{C_l^i}{C_{l^*}^i}\frac{C_{l^*}^i}{C^\circ} \qquad (12)$$

Before computing equation 12 it is possible to simplify equation 5 somewhat. Since $2l^* \gg r$ we can simplify the exp term and see that for all biologically possible values of l*, l, r, V, and P* that the exp term is always less than 1.
So equation 5 reduces to

$$\frac{C_{l^*}^i}{C^\circ} \cong \frac{P^*}{P^* + \frac{Vr}{2l}} \qquad (13)$$

Substituting equations 7, 8, 11, and 13 into equation 12 yields

$$\frac{C_{0.9L}}{C^\circ} \cong \frac{5}{l}\frac{l^*P^*}{P^* + \frac{rV}{2l}}\exp\left(-\frac{2.609L - 2l(1 - \ln l/l^*)}{rV}\right)P^* \qquad (14)$$

(equation 14 has been simplified wherever possible by dropping r whenever it is summed with a larger number such as L, 0.5L, l, l*, etc.

Optimum Permeability for Ambimobility. It will be seen that equation 14 describes a curve with a single maximum when $C_{0.9L}/C^\circ$ is plotted against P* (Fig. 4), *i.e.* there is indeed an optimum permeability for maximum ambimobility. It is therefore of value to derive an equation for computing the optimum P*. This is done by taking the derivative of equation 14 with respect to P*, setting the derivative to zero, and solving for P*.
The answer is

$$\text{Optimum } P^* = \frac{rV}{4l}\left(\sqrt{1 + \frac{8l}{2.609L - 2l(1 - \ln l/l^*)}} - 1\right) \qquad (15)$$

In most cases the term $2l(1 - \ln l/l^*)$ is small compared to 2.6L, so this equation can be approximated to yield

$$\text{Optimum } P^* \cong \frac{rV}{4l}\left(\sqrt{1 + 3.07\frac{L}{L}} - 1\right) \qquad (16)$$

It can be seen that the optimum permeability for ambimobility only depends upon a few anatomical and physiological factors, *i.e.* the over-all length of the plant from apex to root tip, L, the length of the region to which the xenobiotic is confined in the leaf apoplast, l*, the radius of the sieve tubes, r, and the daily average velocity of translocation, V.

Theory for Measurement of Xenobiotic Permeability to Potato Tuber Plasmalemma Membranes. In order to measure the xenobiotic permeability, potato discs of symplasmic volume V_1 and membrane surface area A are placed in a small volume of solution, V_2, containing the substance at initial outside concentration C°. The volume V_2 is about three times V_1. At regular time intervals the external solution is subsampled and C° is measured. The outside concentration C° decreases as the symplasmic concentration C^i increases until at equilibrium $C^i = C° = V_2\ C°\ (0)/(V_1 + V_2)$.

The rate of change of internal concentration, dC^i/dt, is given by

$$\frac{dC^i}{dt} = -\frac{AP^*}{V_1}(C^i - C^\circ) \quad (17)$$

and the rate of change of external concentration, dC°/dt, by

$$\frac{dC^\circ}{dt} = +\frac{AP^*}{V_2}(C^i - C^\circ) \quad (18)$$

Subtracting equation 18 from 17 gives

$$\frac{d(C^i - C^\circ)}{dt} = -\frac{V_1 + V_2}{V_1 V_2} AP^*(C^i - C^\circ) \quad (19)$$

At time 0, $C^i - C° = -C°\ (0)$; at time t, $C^i - C°$ is a smaller absolute difference. Integrating equation 19 from time 0 to t yields

$$\frac{C^\circ - C^i}{C^\circ} = \exp\left(-\frac{V_1 + V_2}{V_1 V_2} AP^* t\right) \quad (20)$$

But $C^i = V_2\ (C°(0) - C°)/V_1$, therefore equation 20 becomes

$$\frac{V_1 + V_2}{V_1}\frac{C^\circ}{C^\circ(0)} - \frac{V_2}{V_1} = \exp\left(-\frac{V_1 + V_2}{V_1 V_2} AP^* t\right) \quad (21)$$

In this derivation we have ignored the volume of water contained in the apoplast and the injured cells on the surface of the potato disc. Nevertheless equation 21 should hold approximately and a plot of the log of the left hand side *versus* time should give a straight line and P* can be evaluated from the slope.

RESULTS AND DISCUSSION

Choice of Parameters. For a passively moving xenobiotic a measure of ambimobility is the ratio $C_{0.9L}/C°$ from equation 14. The larger the ratio the greater the ambimobility. Since it has been suggested that there is an optimum intermediate permeability, P*, for ambimobility, it will be useful to make plots of $C_{0.9L}/C°$ *versus* P* from equation 14. The parameters necessary for this calculation are the characteristic length of the plant's vascular system (L), the length of phloem in the leaf, l, the source zone of the xenobiotic, l*, the radius of the sieve tube, r, and the 24-hr average translocation velocity, V.

The average diameter of 20 sieve tubes in the stem of potato was found to be 11 μm, the range was 8 to 18 μm. With reference to potato plants we will take L in the range of 0.3 to 1.0 m. The maximum length of the carbohydrate loading zone in the leaf blade will be taken as 0.05 m (=l); the xenobiotic is confined to all or part of the leaf 0.005 to 0.05 m (=l*). The 24-hr average translocation velocity (V) will be taken to range from 2.8×10^{-5} to 2.8×10^{-4} m sec^{-1} (approximately 0.1–1.0 m hr^{-1}). So the product of rV will range from $1.5 - 15 \times 10^{-10}$ m^2 sec^{-1} for the purpose of calculations.

Theoretical Ambimobility of Xenobiotics. Figure 3 shows the concentration profiles that would exist in a "linearized" plant 0.3 m long in which the xenobiotic is confined to a 0.05-m-long source zone in the leaf blade. We have plotted the sieve tube concentration C_s^i at distance s relative to the source concentration in the apoplast, C°, *i.e.* $C_s^i/C°$ is plotted *versus* distance, s. In both curves $rV = 1.5 \times 10^{-9}$ m^2 sec^{-1}. In curve A the xenobiotic permeability is near the optimum value, $P^* = 2 \times 10^{-9}$ m sec^{-1}. By the time the sap has passed out of the source leaf, the xenobiotic has not reached equilibrium with the source; $C_l^i/C°$ is only 0.118. In the petiole and stem passive loss leads to a gradual (exponential) decline in concentration between 0.05 and 0.15 m. In the root (0.15–0.3 m) passive loss continues but another effect leads to an increase in concentration. Because we have presumed that the root is a uniform sink for carbohydrate, water will flow out of the sieve tube across the plasmalemma membrane. This water loss contributes to the decline in sap velocity (Fig. 1) and also tends to concentrate the solution faster than passive loss of xenobiotic decreases concentration. The net effect is an accumulation in the root sieve tubes. Water loss of this kind is in accordance with the Münch pressure-flow model (11) or with any model of transloca-

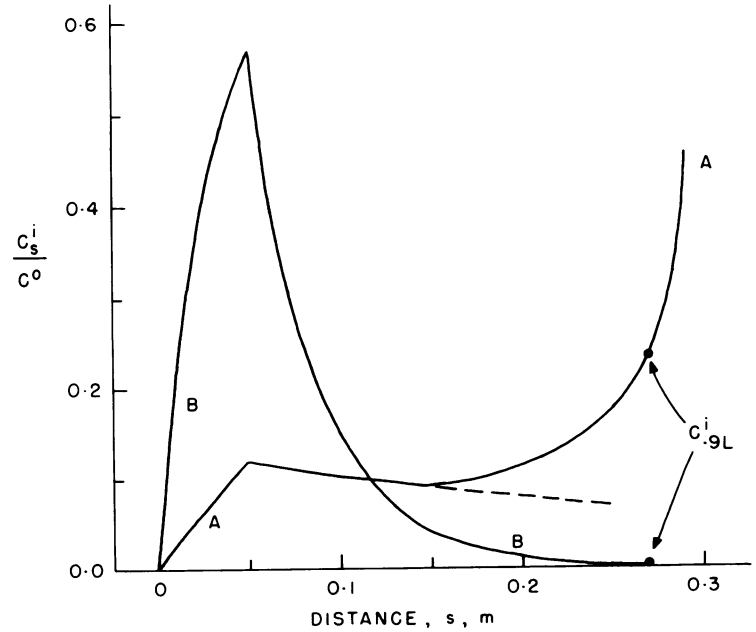

FIG. 3. Theoretical distribution of xenobiotic in sieve tube of a 0.3-m-long "linearized" plant. We have plotted the concentration in the sieve tube at distance, s (=C_s^i) as a fraction of the concentration in the source leaf apoplast, C°. Source is assumed to be 0.05 m long. In this calculation the sieve tube radius times sap velocity, rV, is 1.5×10^{-9} m sec^{-1}. Curve A is for the optimum permeability, P*, of about 2×10^{-9} m sec^{-1}. In curve B P* is 10 times larger, 2×10^{-8} m sec^{-1}. Dashed line extending from curve A shows how $C_s^i/C°$ would decline if V in the root remained constant rather than decrease as in Figure 1.

tion in which sieve tubes are subject to passive osmotic water adjustments due to sugar unloading. If sugar unloading does not occur in the upper part of the root then the sap velocity would not decline and the xenobiotic concentration would decline as in the dashed line. However, there would have to be an even more intense sink farther down the sieve tube which would lead to even more marked accumulations of xenobiotic. Curve B shows what would happen if the permeability were 10 times larger, $P^* = 2 \times 10^{-8}$ m sec^{-1}, but everything else is the same as in Curve A. The higher permeability allows a large passive accumulation of xenobiotic in the source leaf sieve tube, *i.e.* $C_s^i/C^\circ = 0.571$ at s = 0.05 m. But the high permeability also means there is a more rapid loss of xenobiotic in the petiole, stems, and roots. In this case the loss is so rapid in the roots that the concentrating effect of water loss is not enough to exceed the concentration decline due to the more rapid passive loss at the higher permeability.

There is a certain degree of artificiality in the equations that lead to the curves in Figure 3 (and subsequent figures) in so far as it is necessary to specify the length of a discrete xenobiotic source, l^*. A more complete system of differential equations would allow an exact calculation of the apoplastic concentration, C°, as a function of distance. Although the choice of l^* does affect the ratio C_s^i/C° it does not affect the optimum value of P^* very much. For example, if we let L = 0.5 m, l = 0.05 m and $rV = 5 \times 10^{-10}$ m^2 sec^{-1} in equation 15, then the optimum value of P^* for maximum ambimobility is 3.85×10^{-10} m sec^{-1} if $l^* = 0.05$ m and 3.27×10^{-10} m sec^{-1} if $l^* = 0.005$ m. We suspect that a complete solution of the problem would reveal that xenobiotics that are confined to the margins of leaves tend to have permeabilities that are much larger or much smaller than the optimum permeability. If we confine our attention to the concentration ratio at s = 0.27 m = $C_{0.9L}^i/C^\circ$, we can see that there is virtually no accumulation of xenobiotic in this part of the roots when P^* is too large (Fig. 3). A xenobiotic with a permeability of 2×10^{-8} m sec^{-1} would probably be confined to the margin at a high concentration making the source zone much shorter than the 0.05 m indicated. The xenobiotic in curve B would thus be pseudoapoplastic as defined by Edgington and Peterson (5) and it will be apparent later that this permeability is above the optimum. On the other hand, a substance with a permeability much below the optimum would be confined to the margins because the substance would enter the symplasm too slowly to be carried opposite to the transpiration stem in large quantities.

In Figure 4 we confine our attention to the effect of permeability, P^*, on the concentration ratio at a distance of 0.9 times L, where L is the length of the "linearized" plant. In Figure 3 this ratio corresponds to the points marked $C_{0.9L}$. In Figure 4 we have plotted $C_{0.9L}/C^\circ$ *versus* xenobiotic permeability, P^*, through the sieve tube membrane. A major feature of the six plots in Figure 3 is the precipitous drop off of ambimobility at the higher P^* values. At low P^* values, ambimobility also declines but more gradually. The six curves illustrate the impact of sieve tube radius, r, translocation velocity, V, and plant length, L on ambimobility. An increase in r and/or V has identical effects since rV always appears as a product in equation 14. Increasing rV shifts the curve to the right increasing the optimum P without changing the value of $C_{0.9L}/C^\circ$ at the optimum P^*. With reference to equation 15 it can be seen that the optimum P^* increases linearly with rV. Decreasing the over-all length of the transport path, L, shifts the right hand side of the curve up and to the right without affecting the left hand side of the curve.

Ambimobility is not substantially reduced if the xenobiotic is confined to the margins of the leaf rather than the entire leaf blade (Fig. 5). Reducing l^* from 0.05 to 0.005 m reduces the amplitude of the optimum by one order of magnitude. If the xenobiotic is confined to just 10% of the leaf area then C° will be 10 times larger in the margin than if the same quantity of xenobiotic is distributed over the entire leaf blade. So even though $C_{0.9L}/C^\circ$ is 10 times smaller when $l^* = 0.005$ m than when $l^* = 0.05$ m, the net effect is no change in the absolute value of $C_{0.9L}$ because C° is 10 times larger.

In Figure 6 we have plotted the permeability, P^*, for optimum

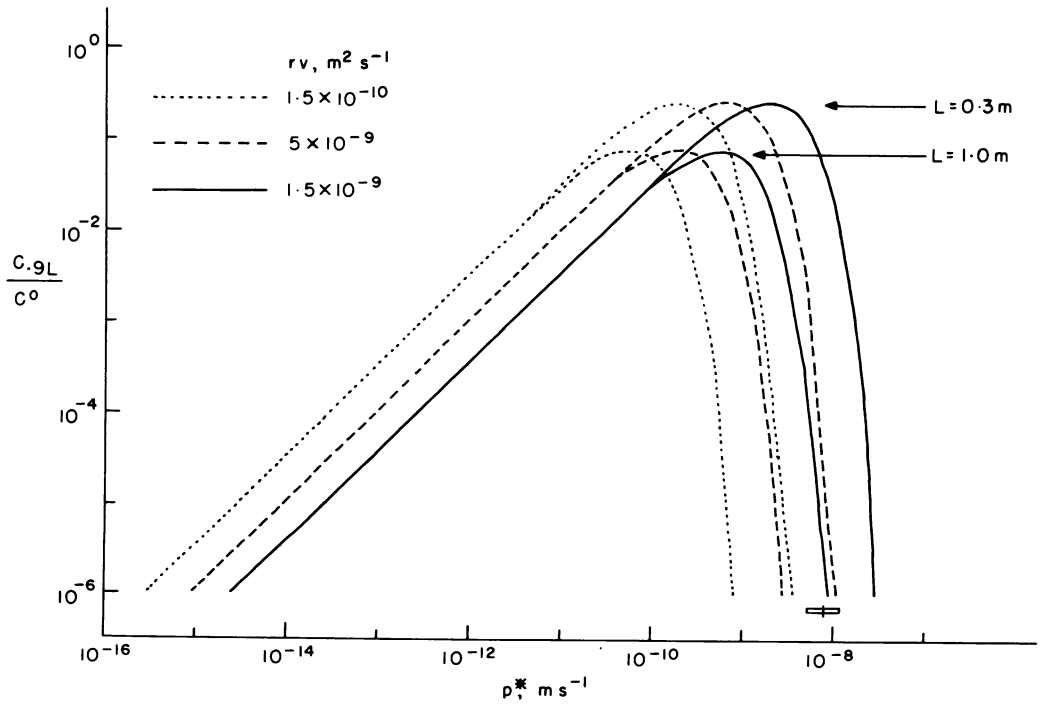

FIG. 4. Effect of permeability, P^*, on passive distribution of xenobiotics as measured by the ratio $C_{0.9L}/C^\circ$ where $C_{0.9L}$ is the sieve tube concentration on the xenobiotic at a distance 0.9 L where L = the over-all length of the plant and C° is the xenobiotic concentration in the apoplast of the source leaf. Curves apply to potato plants of L = 0.3 or 1.0 m and rV ranging from 1.5×10^{-10} to 1.5×10^{-9} m^2 sec^{-1} where r = the sieve tube radius (= 11 μm for potato) and V = average sieve sap velocity (=0.1 to 1.0 m hr^{-1}). Measured value of permeability of oxamyl in plasmalemma membranes of potato tuber parenchyma cells is indicated by horizontal bar in lower right corner of this figure.

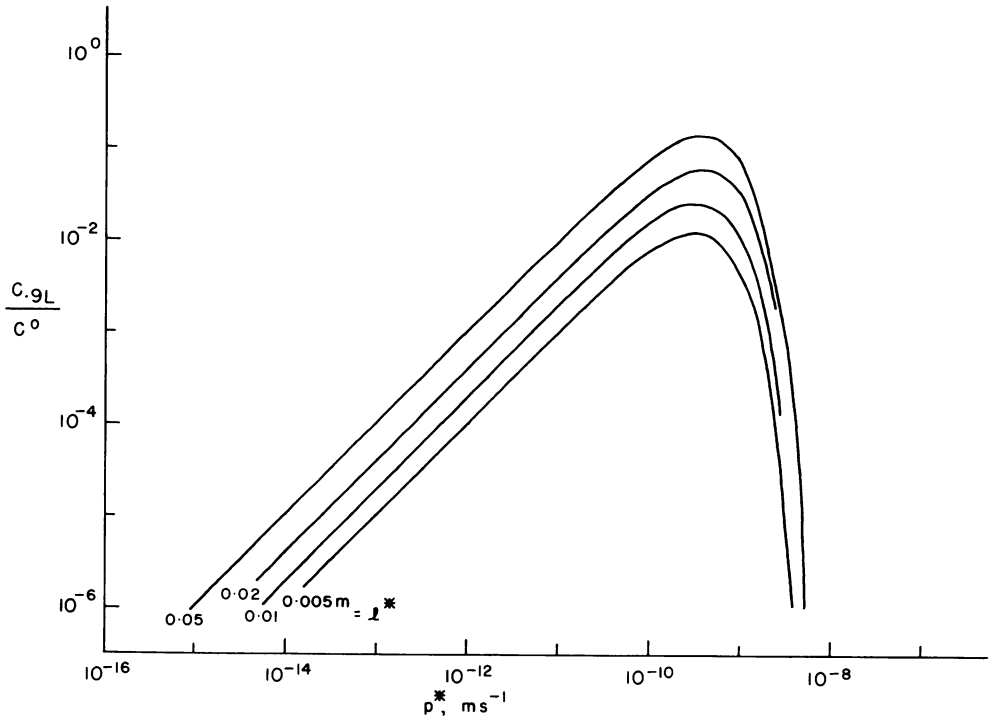

FIG. 5. Effect of various source lengths, l*, on distribution of xenobiotics. rV = 5×10^{-10} m^2 sec^{-1}, L = 0.5 m, l = 0.05 m. Symbols as in Figure 4.

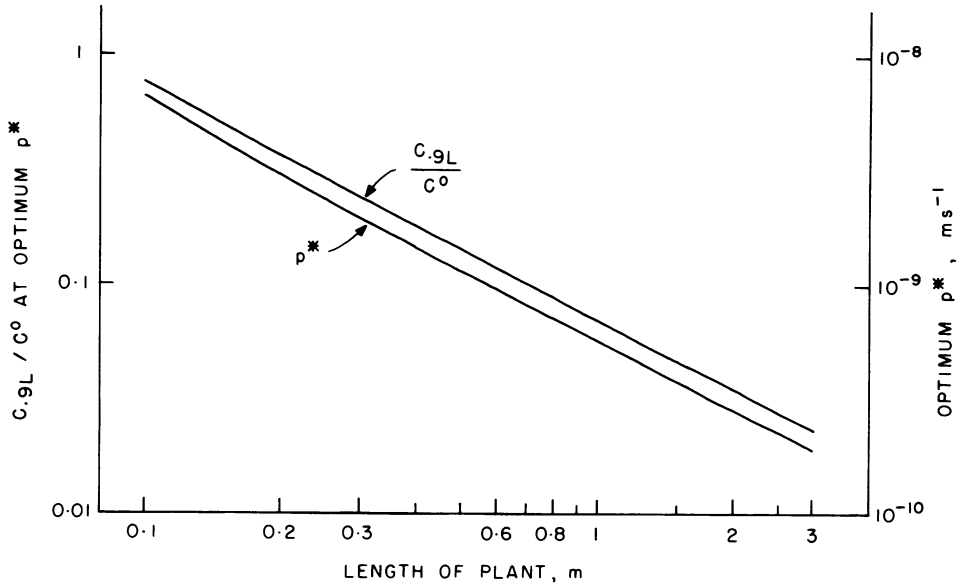

FIG. 6. Dependence of optimum permeability, P*, and $C_{0.9L}/C°$ at optimum P* on plant length L. rV = 1.5×10^{-9} m^2 sec^{-1} and l = l* = 0.05 m. Symbols as in Figure 4.

ambimobility as a function of plant length, L, from equation 15. In these calculations we have taken rV = 1.5×10^{-9} m^2 sec^{-1} and l = l* = 0.05 m. The optimum permeability declines roughly in proportion to the increase in length L. The distribution of the xenobiotic, $C_{0.9L}/C°$, at the optimum permeability also declines in parallel.

Permeability of Oxamyl in Potato Tuber Tissue. Peterson and Edgington (7) have measured the rate of exchange of a number of xenobiotics between discs of potato tuber and a limited volume of bathing medium. Most substances studied exchange rapidly following the same time course. In these cases the rate of exchange is probably limited by diffusion through unstirred layers and the apoplast. Oxamyl exchanges more slowly and may therefore be limited by its permeability in the plasmalemma membranes of the parenchyma cells of the potato tuber. The equations governing this membrane-limited exchange are derived under "Theory for Measurement of Xenobiotic Permeability to Potato Tuber Plasmalemma Membranes" in the theory section. Potato discs of approximately 0.0013 kg fresh weight were placed in about 3.5×10^{-6} m^3 of solution containing oxamyl. The dry weight of potato tuber makes up 14% of the fresh weight, so we estimate the water content of the discs to be 0.86 × the fresh weight; so the ratio $(V_1 + V_2)/V_2$ in equation 21 is approximately 4.6/3.5 where V_1 = the symplasmic water volume and V_2 = the volume of the bathing medium. The parenchyma cells of potato tubers are globular and the mean diameter of 24 cells was measured to be 124 μm with a range of 78 to 170 μm. The surface to volume ratio A/V_1 of equation 21 can be estimated by spherical geometry or cubic geometry to be equal to 6/d where d is the diameter = $6/1.24 \times 10^{-4} = 4.84 \times 10^4$ m^{-1}.

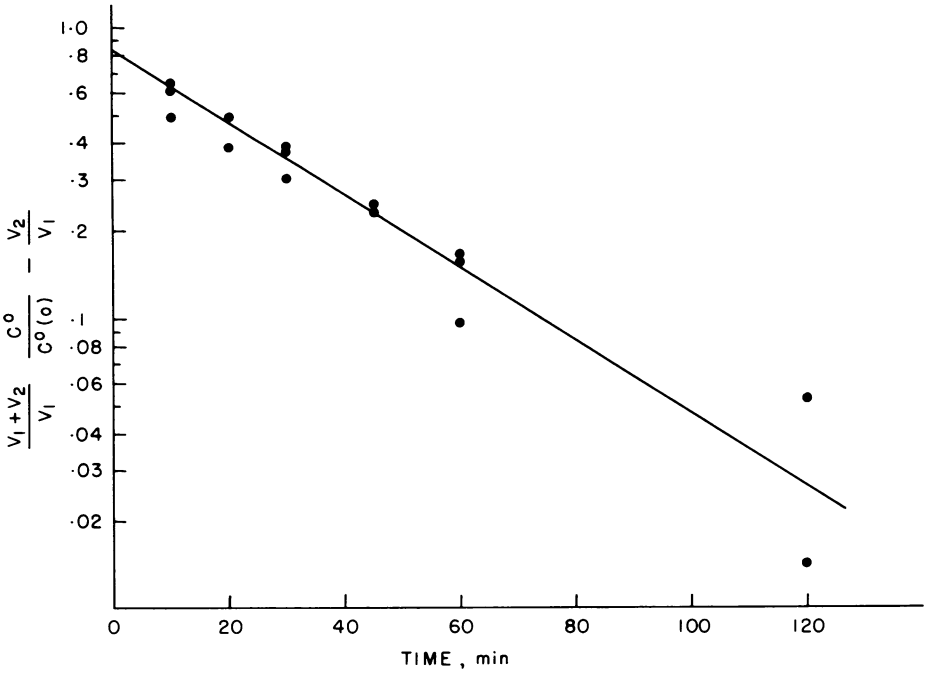

FIG. 7. Influx of oxamyl into potato tuber discs from a small volume of solution. Each dot represents mean of four replicates. C° (0) is starting concentration of oxamyl in bathing medium of volume V_2 at time zero. V_1 is volume of symplasm of potato discs. C° is concentration in bathing medium at later times plotted on abscissa.

A plot of the left hand side of equation 21 *versus* time, t, should yield a straight line, and this is borne out by the actual experimental data (Fig. 7). The half-time, $t_{1/2}$, is 23 min = 1380 sec. The permeability, P*, can be calculated from the half time by use of equation 22.

$$P^* = \frac{V_1}{A} \frac{V_2}{V_1+V_2} \frac{\ln 2}{t_{1/2}} \qquad (22)$$

Our best estimate of P* from Figure 5 is $P^* = 7.9 \times 10^{-9}$ m sec^{-1}. This estimate of P* is plotted on Figure 3. Even allowing for a possible error of ±50%, it can be seen that the calculated P* is outside of the range of most of our values of the theoretical optimum P*. The permeability of oxamyl to the plasmalemma membranes of potato tuber parenchyma cells is approximately 10 times too large to permit ambimobility in adult-size potato plants (1 m) when the 24-hr average translocation velocity is about 0.3 m hr^{-1}.

Why did Peterson *et al.* (6), find about 7% of the total applied oxamyl in the roots of potato plants after application to the mature leaves? Part of the explanation would appear to be that they used small plants only 5 weeks old and having a typical length of 0.3 m. Also, the plants were grown in a greenhouse with continuous supplementary light 24 hr/day. Thus we might expect the translocation velocity to be near the peak value all of the time (perhaps 1 m hr^{-1}). This corresponds approximately to the curve in the upper right of Figure 3 and it can be seen that the measured permeability of oxamyl is near the optimum value of this curve.

The attentive reader may have other reservations concerning the accuracy of our model due to its oversimplification into an unbranched sieve tube of uniform diameter. It is well known that the sieve tubes in minor veins of some plants are of smaller diameter than those in the major veins. In our opinion, there is no advantage in modeling for this because we do not know how the diameter increases with distance in any plant, and because the multiple branching of minor veins which could also change the quantitative conclusions is even less known. The qualitative effect of having many branched minor veins of small diameter would be to favor symplasmic uptake there and therefore ambimobility. Another questionable factor is the velocity profile in the leaves and roots. If the velocity does not change linearly as in Figure 1, how does this affect optimum permeability? We can get some insight into this by taking an opposite extreme for the profile. If the velocity is the same everywhere it can be shown that the expression analogous to equation 15 for the optimum permeability is

$$\text{Optimum } P^* = -\frac{rV}{2L} \ln\left(1 - \frac{L}{0.9L}\right) \qquad (23)$$

Putting numbers into this equation reveals that the effect is to shift the optimum value of P* up by less than a factor of 2. We conclude that the exact velocity profile is of minor importance.

We felt that the theory is close enough to reality to merit further consideration. If the theory is right, a xenobiotic chemical should have a permeability of about 3×10^{-10} m sec^{-1} to be most effective for the widest variety of plant sizes and translocation velocities. It is probably better to have a P* a bit low for short plants so that optimum protection is provided to tall plants (Figs. 4 and 6). It is possible that the permeability of sieve tube membranes is smaller than parenchyma cell plasmalemma membranes. But we think this is unlikely. The theoretically permissible permeabilities of sieve tube membranes to water and sucrose do not have to be unusually low for the Münch pressure-flow hypothesis (11), so there is no *a priori* reason why sieve tube membranes should be unusual in terms of passive permeability properties.

In summary, it seems that there is an optimum permeability for the ambimobility of xenobiotics. The value of the optimum permeability depends on just a few characteristics of the plant: the 24-hr average velocity of translocation, V, the average sieve tube radius, r, the length of the vascular system, L, and the length of the (sucrose) source region in the leaf (equations 15 and 16). Consequently it is not theoretically possible to devise a xenobiotic which will be optimally ambimobile for plants of all sizes. The optimum permeability of a small plant is greater than the optimum permeability of a large plant.

It is frequently found that xenobiotics are confined to the margins of leaves by the transpiration stream. Our theory reveals that this, in itself, does not reduce the ultimate concentration of xenobiotic in the root phloem, $C^i_{0.9L}$; however, we suspect that

substances confined to margins probably have permeabilities much larger or smaller than the theoretical optimum and should therefore be avoided.

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