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Mechanisms of Translocation of Plant Metabolites

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I. INTRODUCTION

The mechanism of translocation has been discussed since the latter part of the 19th Century, when DeVries, in 1885, proposed protoplasmic streaming as the mechanism. Since that time O. F. Curtis, beginning about 1920, and more recently Thaine (1961) and Canny and Phillips (1963) have become interested in this approach to the problem. In the meantime Münch, in 1930, proposed a pressure flow mechanism based on a turgor pressure gradient in the phloem between metabolite supplying and metabolite consuming areas. These two mechanisms, and others, are fully discussed in Swanson (1959), so the present paper will deal with a compilation of the factors upon which a sound view of mechanisms must rest. It does not seem possible to arrive at a decision as to mechanisms on the basis of any narrow approach to the subject. The distribution system itself is complex in its cellular make-up, ramifies to all parts of the plant body, and lacks a centralized pumping mechanism. For these reasons it is considered, by most workers in the area, that a very broad knowledge of the plant and its processes is necessary if one is to evaluate the phenomenon of translocation fruitfully.

The most recent comprehensive treatment of the broad considerations of translocation is that of Kursanov (1963). Proceeding backwards there are the reviews of Crafts (1961), Swanson (1959), and Biddulph (1959). The most comprehensive mathematical treatment is that of Horwitz (1958), but specialized applications to particular aspects of translocation can be found in Preston (1963) and Canny and Phillips (1963).

Because of limitations of space and other reasons the work on translocation of herbicides is not included (see Crafts, 1961 for this) nor is much attention given to two, as yet, anomalies in the literature. These are the very rapid translocation rates reported by Nelson et al. (1958), and the "transcellular strand" view of Thaine (1961). In regard to the first, our early experiences with $^{14}\text{CO}_2$ and THO led us to the adoption of triple seals between application and target organs in order to avoid

artifacts due to external convection. The work of Nelson et al. needs verification using equal precautions, but it should be emphasized that neither the profiles, (Horwitz, 1958) nor the amount moved (Nelson et al., 1958) are right for this to be the main stream of translocation.

Regarding Thaine's transcellular strands—I think more positive evidence for their existence is necessary before a mechanism of translocation is based upon them. The translocation profiles worked out by Canny and Phillips (1963) for Thaine's model are not sufficiently different from Horwitz's treatments of pressure flow and cyclosis-diffusion, to expect that acceptance or rejection can be reasonably based on profiles. Also the calculated rate of movement by transcellular streaming is too slow to fit the known rates of movement.

II. ANATOMY OF THE PHLOEM

One of the important points bearing on the hypotheses concerned with translocation mechanisms is the condition (size) of the openings in the sieve plate, and the degree of continuity of movement that is possible between successive members of the sieve tubes. It should be emphasized that the volume and velocity of flow is known to be sufficient to require that the anatomical features of the conduits do not deter this flow in a serious manner. The work on the sieve-tube members with conventional histological procedures has therefore caused much confusion because it has consistently shown the pores in the sieve plates to be closed. It is now reassuring that newer work with the electron microscope shows that the pores, in those plants that have been so examined, are indeed open.

Duloy et al. (1961) using *Cucurbita pepo* (Duchesne) described a parietal layer of cytoplasm as lining the sieve plate and extending as a lining to the open sieve pores. There was no closing layer or membrane across the sieve pores. Individual elements are continuous with each other—via the open sieve pores, forming a conduit, the sieve tube. The absence of a typically organized cytoplasm with organelles suggested to these authors that the sieve tubes were metabolically inert, and that it was the companion cells that possessed the cytoplasmic organization and components capable of a high metabolism. Kollmann (1963) has compared the structural features of dormant and reactivated sieve cells of *Metasequoia* and has shown the presence of plastids, mitochondria, endoplasmic reticulum, and nucleus. The changes observed in the transformation from dormant to active include a change from regular tubules of endoplasmic reticulum to dilated tubules with "cisternae" and local swellings which apparently disintegrate into numerous separate vesicles. In addition to these vesicles, well-differentiated lamellar bodies derived from either form of the endoplasmic reticulum appear, and what is most significant, were found to traverse the pores in the sieve plates. After this comparison with his earlier work on *Passiflora caerulea* (1960), Kollmann expressed the conclusion that these tubules arose from the endoplasmic reticulum. Arrigoni and Rossi (1965) using *Avena coleoptile* for studies of fine structure of sieve tubes found that the strands con-

necting the sieve-tube members with each other (through the sieve plate) were produced by a double membrane system very similar to the endoplasmic reticulum. This constituted cytoplasmic continuity between cells.

Cronshaw and Esau's (1967) observations are also compatible with the view that the contents of contiguous mature sieve elements are continuous through the sieve-plate pores, and Esau et al. (1966) have reported the movement of virus particles through the pores. This step in bringing anatomical observations into closer alignment with physiological observations is helpful in that it materially reduces the calculated energy expenditure necessary to account for passage of solute through the sieve plate.

III. LOADING OF THE PHLOEM

The movement of photosynthate, or metabolites from the surrounding mesophyll cells of the leaf into the conducting tissues of the phloem is known as "loading" and has been investigated to some extent. The transfer is known to be rapid, requiring only a few minutes (2 to 3 min in rhubarb [Kursanov et al., 1959] and less than 10 min in maize [Pristupa, 1964]) from $^{14}\text{CO}_2$ to labeled metabolite in the conducting phloem. The process of loading is selective, as shown by the failure of certain sugars and organic acids to be transferred while others moved in readily (Kursanov et al., 1959). As a further example the amino acids threonine and to a lesser extent serine and alanine were shown to move into the sieve tubes rapidly whereas others including aspartic acid and proline moved in more slowly (Kursanov and Brovchenko, 1961).

Entrance into the sieve tubes is apparently independent of concentration differences between mesophyll and sieve tubes in the case of sucrose (Canny, 1961), amino and organic acids (Kursanov and Brovchenko, 1961), and phosphorylated sugars (Ziegler, 1956). It is apparently quite consistent with these data to view the movement of sugars to the sieve tubes as occurring in the phosphorylated form with synthesis of sucrose occurring as a last step before or during entrance into the sieve tubes (Pavlinova, 1955).

Both the process of transport to the sieve tubes and the terminal step of passage into the sieve tubes may require ATP (adenosine triphosphate) (Kursanov and Brovchenko, 1961; and Shiroya, 1968). A separation of the two processes, i.e., movement to and secretion into the sieve tubes, has not been satisfactorily attained, but Kursanov and Brovchenko's results strongly suggest a final loading via the energy source of ATP. This loading also appears to be sensitive to O_2 shortage and to metabolic inhibitors (Leonard and Glenn, 1968).

Age may also be a factor in loading of the phloem both as to the time course of loading (Kursanov and Brovchenko, 1961; Nelson, 1962; Ursino et al., 1968) and as to the types of materials loaded (Biddulph and Cory, 1965), but data on the latter point are limited.

Table 7-1—Sugars in sieve-tube exudate of some American trees
(from Crafts, 1961)

Family	Name of tree	Sucrose, %	Raffinose, %	Stachyose, %	Verbascose, %
Salicaceae	Aspen (<i>Populus tremuloides</i>)	10-25	< 0.5	< 0.5	0.5-0
Fagaceae	Beech (<i>Fagus grandifolia</i>)	10-25	< 0.5	0.5-0	0.5-0
	Chestnut (<i>Castanea dentata</i>)	10-25	< 0.5	0.5-0	0.5-0
	White oak (<i>Quercus alba</i>)	10-25	0.5-0	0.5-0	0.5-0
	Chestnut oak (<i>Q. prinus</i>)	10-25	0.5-0	0.5-0	0.5-0
	Red oak (<i>Q. rubra</i>)	10-25	0.5-0	0.5-0	0.5-0
	Elm (<i>Ulmus americana</i>)	2-10	2-10	2-10	0.5-0
	Tulip tree (<i>Liriodendron tulipifera</i>)	10-25	< 0.5	< 0.5	0.5-0
Magnoliaceae	Black cherry (<i>Prunus serotina</i>)	10-25	< 0.5	0.5-0	0.5-0
Rosaceae	Black locust (<i>Robinia pseudo-acacia</i>)	10-25	0.5-0	0.5-0	0.5-0
Leguminosae	Striped maple (<i>Acer pennsylvanicum</i>)	10-25	< 0.5	0.5-0	0.5-0
	Sugar maple (<i>Acer saccharinum</i>)	10-25	0.5-0	0.5-0	0.5-0
Rhamnaceae	Buckthorn (<i>Rhamnus cathartica</i>)	10-25	< 0.5	< 0.5	0.5-0
Tiliaceae	Basswood (<i>Tilia americana</i>)	10-25	< 0.5	< 0.5	0.5-0
Nyssaceae	Blackgum (<i>Nyssa sylvatica</i>)	10-25	< 0.5	0.5-0	0.5-0
Oleaceae	White ash (<i>Fraxinus americana</i>)	2-10	2-10	10-25	< 0.5

IV. MATERIALS TRANSLOCATED

The principal carbohydrate translocated in the sieve tubes appears to be sucrose, but in trees and some other plants this molecule may have condensed with it one or more molecules of galactose, to give raffinose, stachyose, or verbascose in order of decreasing concentrations (Table 7-1).

Sucrose is also the principal carbohydrate translocated in herbaceous plants. Amino and organic acids, minerals, viruses, hormones and steroids are also known to be translocated. As sucrose moves through the sieve tubes it may be withdrawn into surrounding cells and hydrolyzed there so that whole-phloem analysis may give misleading results. One of the most convincing demonstrations that sucrose is the translocatory substance with glucose and fructose the products of its breakdown in surrounding tissue is that of Biddulph and Cory (1965). Here $^{14}\text{CO}_2$ and ^{32}P were given to a leaf simultaneously. The labeled sugar, sucrose, and the sugar phosphates, glucose-6, PO_4 and fructose 1-6, diPO_4 , were isolated from whole phloem of the stem below the leaf, but whereas the P^{32} (as phosphate) moved with the sucrose in the sieve tubes none of the glucose-6, PO_2 or fructose 1-6, diPO_4 isolated from whole phloem contained the P^{32} label. This led to the conclusion that they had been phosphorylated outside the sieve tubes with indigenous (not translocatory) phosphate. Swanson and El-Shishiny (1958) have also supplied convincing evidence that sucrose is the translocatory substance and that the presence of glucose and fructose represent hydrolytic products outside of the sieve tubes.

Studies of enzymes associated with phloem tissues are still largely descriptive and until more refined methods are devised that permit *in situ* studies, or studies of organelles isolated from specific cell types it is doubtful that much additional useful information on mechanisms of transport will be obtained. Kursanov (1963) has included a summary of this topic, so no further review will be made here.

V. LINEAR RATE OF MOVEMENT

There are sufficient studies on the rate of movement in the phloem to establish some minimal values. For sucrose this rate is often in excess of 100 cm/hr. Some representative values are presented below:

Plant	Rate, cm/hr	
Metasequoia	48-60	Willenbrink & Killman, 1966
Potato (<i>Solanum tuberosum</i> L.)	20-80	Mokronosov & Bubenschikova, 1962
Sugar beet (<i>Beta vulgaris</i> L.)	50-135	Mortimer, 1965
Bean (<i>Phaseolus vulgaris</i>)	107	Biddulph & Cory, 1957
Cucurbita	250-300	Webb & Gorham, 1965
Wheat (<i>Triticum aestivum</i> L.)	100	Wardlaw, 1965
Sugarcane (<i>Saccharum officinarum</i> L.)	240-360	Hatch & Glasziou, 1964

There are technical reasons why the velocities (or rates) must be given in minimal values when determined by the movement of tracer assimilates. There is always attenuation at the front of the tracer stream by a lateral loss of the tracer from the sieve tubes which causes the marker to fall further and further behind the theoretical rate of movement (Biddulph and Cory, 1957; Horwitz, 1958; Spanner, 1963). The technical mathematical treatment of attenuation and loss will not be considered here, for both would appear to alter rates by relatively small amounts (except, perhaps, for a diffusible substance like water), and velocities are not completely accurate in most cases, for they include a photosynthetic incorporation of $^{14}\text{CO}_2$ and movement of the photosynthate to the sieve tubes.

VI. DISTRIBUTION

The destination of metabolites exported from a given leaf depends upon the leaf's position. In the bean plant, lower leaves export primarily to the root with a small fraction ascending to the apex. From the uppermost exporting leaves the flow is chiefly to the apex. Intermediate leaves may export in both directions. Similar patterns of distribution have been reported for soybean (*Glycine max* L.) (Thrower, 1962), grape (*Vitis vinifera*) (Hale and Weaver, 1962), cotton (*Gossypium hirsutum* L.) (Tulichbaev and Kruzhilin, 1965), and tea (*Thea sinensis* L.) (Sanderson and Sivapalan, 1966).

It cannot be emphasized too strongly that a knowledge of the anatomy of the phloem of the plant under study is prerequisite to understanding distribution phenomenon. It is known that there is a relatively strict or direct functional channel between a particular part of a root system and a corresponding part of an aerial organ. The best data are for minerals locally absorbed by selected regions of the root (Biddulph, 1959). There is also a similar strict relationship between metabolite-supplying and metabolite-using parts, as assimilates from mature leaves move only to immature ones of the same orthostichy (Jones et al., 1959 and Kursanov, 1963).

Joy (1964) has shown that in sugar beet plants an older leaf will translocate to younger ones directly above it (on the same side of the stem) but not to leaves located on the far side of the stem. However, movement into young leaves on the opposite side of the stem could be forced by removing the intervening leaves—leaving the young leaves dependent on a supplying leaf on the opposite side of the stem. Shiroya et al. (1961) have shown a similar phyllotaxic relationship between the supplying leaf and the receiving leaves on tobacco (*Nicotiana tabacum* L.). Some tangential movement occurred, but leaves on the opposite side of the stem from the supplying leaf failed to acquire the tracer. Partial girdles made in phloem to interrupt the normal flow of metabolite between a particular source and sink have been shown to result in the development of new phloem (from parenchyma cells) around the girdle. Most experimentalists consider that the distribution of metabolite between source and sink is controlled by the gradient between the two areas. The rapidity of flow toward a given sink is determined by the

steepness of the gradient, and the gradient is made steeper by the unloading, or removal, process at the sink. Experimental control over gradients by direct means has, however, not been satisfactorily attained.

VII. RADIAL LOSS FROM THE PHLOEM

During the course of movement of metabolite in the phloem some withdrawal for storage in or nutrition of adjacent tissues occurs, and if there is sufficient radial movement some may even ascend in the xylem. If a distinct cambium is present a radial loss of tracer from the phloem bundles can be determined by the separation of xylem from phloem and the determination of the amount of tracer in adjacent sections. This type of study has shown the radial loss to be some function of the amount of tracer moving in the phloem. This relationship is, in turn, responsible for the development of the generalized logarithmic pattern of tracer as it moves through the phloem (Biddulph and Cory, 1957). Stated simply, there is a linear relationship between the logarithm of the concentration present and the distance of movement. These losses can be significant, i.e., up to 49% of the total labeled metabolite at the position just below the node of a newly exporting leaf, diminishing progressively to 4% in the internode below the primary leaves (Biddulph and Cory, 1965). Losses to the xylem of approximately 24% of the ^{14}C metabolites and ^{32}P during a 60-min migration period in the internode below the first trifoliate leaf of a bean plant (and 25% for a comparable position in a cotton plant) have also been reported (Biddulph and Cory, 1965 and Biddulph and Markle, 1944). When the loss was high, i.e., 49%, the metabolite was rich in steroid and contained 12 other labeled substances besides sucrose; but which substances left the phloem was not determined.

Tritiated water moving in the phloem also crosses to the xylem in amounts up to 31% during a 20-min migration period. Such a significant loss, in this case probably representing a continuous exchange with indigenous water, may explain why labeled water movement in the phloem presents some patterns different from that of sucrose and other tracers (Biddulph and Cory, 1957; Gage and Aronoff, 1960; Choi and Aronoff, 1966; and Trip and Gorham, 1968). Actually the plasmalemma of sieve-tube members should be permeable to water even though they are quite impermeable to sucrose.

Webb and Gorham (1965) have measured the velocity of the radial movement in squash plants and have found that there was variation with age of the tissues. Young petioles displayed maxima of 6 cm/hr while older ones showed 1 cm/hr. The principal sugar in lateral movement was sucrose, whereas for longitudinal movement it was stachyose, illustrating differences in lateral loss of the two sugars from the phloem. Radial movement to the central pith of the potato plant was also shown by Mokronosov and Bubenschikova (1962).

Horwitz (1958) and Spanner (1963) have presented a mathematical treatment of tracer distribution in the stem during its course of movement. Both studies show that there will be a deviation from the logarithmic pattern if any of the following conditions do not remain constant during the experimental period: the rate of entrance of tracer into the

phloem; the cross-sectional area of the conduits; the lateral loss at different levels; the velocity of flow at different levels. To the present time, satisfactory mathematical studies with these factors as variables have not been made. One of the reasons why a more refined analysis has not been attempted is that the anatomy of the phloem system itself, and consequently the flow pattern, may contribute a variable of greater magnitude than any of the above factors. The types of irregularities in phloem movement will become apparent under the following treatment of tangential movement.

Fig. 7-1—The fluoresced phloem at the first trifoliate leaf node of a bean plant. Numbers 1 through 6 identify the leaf traces by the broken stubs of the xylem components. The branch gap is identified by the number 7. A longitudinal slit along leaf trace number 3 was necessary to flatten the section for photography. In the following figures the slit was made into the branch gap from above for the same reason. The figure represents the phloem as viewed from the inner face. The sheathing cylinder of "bark" has been slit, peeled off, fluoresced, and laid open for viewing (see Biddulph and Cory, 1965). For callose fluorescence see Currier and Strugger, 1956.

VIII. TANGENTIAL MOVEMENT

Tangential movement from a particular phloem bundle to an adjacent one would result in a more or less direct intercontamination of the two streams. This would mean that only a generalized rather than a strict nutritional interrelationship would exist between exporting and importing parts. We have ample evidence that the relationship is a rather strict

Fig. 7-2—An autoradiogram (reversed) representing the flow of metabolite (in the phloem) from the first trifoliate leaf. Metabolite entered in leaf traces 1 through 6 at the node in upper figure A. It descended to the primary leaf node at lower figure A. A fraction of the metabolite then ascended in bundles alternating with the leaf traces back past the node of entrance and on up past the second trifoliate leaf node in upper figure B. The descending leaf traces from the second trifoliate leaf are lettered A through E (Fig. 7-2B) and can be followed downward to the first trifoliate leaf node. They do not conduct labeled metabolite into the second trifoliate leaf: From Biddulph and Cory, 1965.

one, both for the xylem system (Roach, 1939) and for the phloem system (Biddulph and Cory, 1965; Kursanov, 1963).

Fig. 7-1 shows the phloem pattern at the node of the beam stem and 7-2 shows how strictly the labeled photosynthate follows the phloem channels. The leaf traces carry the labeled metabolite to the first node below the point of entrance into the stem, and from here, by means of anastomoses, the metabolite may move tangentially into adjacent phloem bundles where a portion of it may ascend the stem back up past the node of entry and into the internode above (Fig. 7-2B). The metabolite stream then ascends past the next higher node without delivering metabolite into the leaf.

Fig. 7-3 shows what happens to the ascending metabolite as it approaches a young leaf that is just changing from an importing to an exporting organ. By comparing the vascular anatomy shown by fluorescence in A) with the autoradiogram (B) it can be seen that there is only the slightest indication of import into this leaf.

Finally, when the destination of the initial export from a newly matured leaf is examined it is evident that most of the metabolite ascends in the phloem to the immature leaves and bud at the stem tip, Fig.

Fig. 7-3—The fluoresced phloem A and the corresponding autoradiogram B at the node of a young leaf that is just changing from an importing to an exporting leaf. The metabolite in Fig. 7-3B is ascending in the phloem from a lower leaf. There is only a very slight indication that metabolite is entering this leaf. The arrows indicate a possible importing phloem bundle.

7-4. A downward flow in the leaf traces from this newly exporting leaf extended for only approximately 25mm during the experimental period. A chromatographic examination of the composition of the labeled metabolite from similar newly exporting bean leaves showed fourteen ^{14}C labeled compounds to be present, but of these fourteen steroid was initially the preponderant one. A time sequence study of the labeling of the first exported metabolite showed (i) that upward export always preceded downward export; (ii) that upward export consisted of labeled metabolite rich in steroid; (iii) that approximately 2 hours were required for $^{14}\text{CO}_2$ to be incorporated into steroid and for the labeled steroid to appear in

Fig. 7-4—(A) A gross autoradiogram (life size) of the very young fourth trifoliate leaf and stem apex showing the path of labeled metabolite originating from the third trifoliate leaf as it first began to export. The position of the exporting leaf, the third trifoliate leaf, is shown by the arrow in Fig. 7-4B. (B) An autoradiogram (considerably enlarged) of the frozen-dried stripped bark above and below the third trifoliate leaf node. A and B are contiguous sections; upper B joining lower A. The principal export from the young third trifoliate leaf was upward (from Biddulph and Cory, 1965).

the exported metabolite; (iv) that after sufficient maturity the labeled export was preponderantly sucrose, and that it moved downward a full node before ascending to the stem tip; and (v) that the labeling time from $^{14}\text{CO}_2$ to ^{14}C sucrose, when it finally appeared in the stem in large quantity, was less than 15 min.

The direct upward movement of steroid from the node of the newly exporting leaf took place in the phloem. This means that at the node, where the cauline phloem bundles pass under (on the cambial side) the phloem bundles in the leaf trace girdle, there was a direct transfer of this lipid-soluble fraction into the cauline bundles. The detailed autoradiogram in Fig. 7-5 contains a representation of this type of direct movement.

Related to the topic of tangential movement is the subject of simultaneous import into and export from a given leaf. Of five papers dealing with this subject all agree that older leaves either do not import (Biddulph and Cory, 1965; Sanderson and Sivapalan, 1966; Jones et al., 1959; Williams, 1964) or import only traces of metabolite (Thrower, 1962. Williams and Thrower claim there is a short period wherein a

Fig. 7-5—The fluoresced phloem and the corresponding autoradiogram showing the export of ^{14}C -labeled metabolite from a young but well established exporting leaf. The entrance of metabolite from the leaf is through the two halves of the slit petiole base indicated by the arrows. Most of the metabolite descends in the leaf traces, but a small amount is shown crossing directly into cauline bundles and ascending toward the apex.

newly maturing leaf may import as well as export. Two points need be made from these data. First, import of metabolites into mature leaves appears to be limited to that fraction that moves rapidly from the phloem during its course of descent and on entering the xylem may ascend into a mature leaf. Second, if a leaf both imports and exports simultaneously there occurs what is designated as bidirectional movement in the petiole. This may be possible for a short time since growth of a leaf may not be uniform throughout so that while one portion is still importing another may have matured sufficiently to have begun exporting. This would mean that adjacent phloem traces may be supplying and delivering metabolite at the same time. The duration of such a condition, however, must be relatively short. The phenomenon will be referred to again under bidirectional movement.

The origin of nonuniformities in the distribution pattern along the stem can easily be understood when the general pattern of movement of metabolite from a single leaf is considered in relation to the pattern of phloem bundles through which it moves. In many instances the flow becomes divided in a rather complex way, some of it ascending from various nodes and some of it continuing on toward the root. Within a given internode, then, there may be descending and ascending streams—the ascending stream having been withdrawn from an originally descending stream and on ascending it increases the total mobile metabolite in the internode above while it decreases the amount that continues downward by a like amount. If radial loss also occurs, and is some variable function of the amount moving in the sieve tubes, it is to be anticipated that still greater irregularities in the distribution profile will be found. Such irregularities have been observed by many experimentalists and they illustrate the reason why a mathematical treatment of distribution in the stem must be viewed with caution when such a treatment is used as a guide to discriminate between mechanisms of translocation. The specific reason for the inclusion of the autoradiograms in Fig. 7-1 to 7-5 is to illustrate distribution patterns and some of their complexities, and to show the integrity of the phloem system as a conduit for metabolite flow.

IX. REMOVAL FROM THE PHLOEM

The withdrawal into surrounding tissues of substances (largely sucrose) from the phloem appears to be regulated as completely and in much the same fashion as their entrance into it. The process has been studied more indirectly than directly, but to date the studies show the uptake into the surrounding tissues to consist of a two-phase system with a non-metabolic and a metabolic phase (Bialeski, 1962). Absorption into the nontranslocating tissue proceeds at different rates for different sugars (Glasziou, 1960), and the internal concentration of a given sugar with respect to another, e.g., sucrose, to fructose, remains the same even when the relative external concentration is varied greatly.

In sucrose storing tissue, such as paranchuma, the sucrose will be equally labeled in the two hexose moieties regardless of which of the externally fed hexose precursors, fructose or glucose, carries the label (Glasziou, 1960; Pavlinova, 1955). The synthesis of the sucrose stored

in the "inner" space therefore involves isomerization and polymerization at or within the boundary separating the two spaces, inner and outer. The absorption into the storage cells is selective, in that there is competition between sugars for carrier (Bielecki, 1960a; Glasziou, 1960), and absorption can be inhibited by KCN, Na-azide, monoiodoacetate and chloramphenicol (Bielecki, 1960b).

The topics of "loading" and "unloading" are not intended to be presented as exhaustive surveys as this subject is covered elsewhere in this book. The important relationship to translocation phenomenon is simply that the loading and removal from the translocation stream, both active processes, help to maintain the gradients essential to movement of substances in the sieve tubes. The capacity for an isolated section of phloem to accumulate sucrose (Bielecki, 1966) and to build up a pressure sufficient to maintain a flow of solution through aphid stylets penetrating the sieve tubes (Weatherly et al., 1959) should be considered as being particularly revealing and of great importance in understanding the overall mechanics of translocation.

X. MECHANICS OF TRANSLOCATION

There are so many aspects of the translocation phenomenon, each related to some vital part of the whole, that it still seems impossible to formulate a clear statement of the mechanics of the process. The heart of the matter is, of course, the mechanism that propels the materials—metabolite, minerals, regulatory substances, virus particles etc.—across the sieve plates, for if it were not for this resistance to movement the Munch hypothesis would appear adequate. Actually there exists in the phloem all of the requisites of an osmotic system; a sucrose injection process, a system of tubular conduits in which longitudinal flow usually far exceeds lateral losses, and a sucrose removal system that is particularly strong at the extremities of the conduit system. It just seems unrealistic not to recognize in this at least the rudiments of the Munch system—yet there exists the hard facts of the high theoretical resistance that should be offered by the sieve plates, if they are structurally as pictured by anatomists. For the sieve tubes to function in the Munch manner the resistance offered to flow through each sieve plate must somehow be substantially reduced or some other compensating factors must be disclosed.

It is generally agreed that the rate of assimilate flow in the phloem is slow enough that laminar flow through the sieve plate may occur—if the pores are open and they collectively constitute a reasonable percentage of the cross-sectional area of the sieve tube.

Horwitz (1958) has shown that if a solution flow were to take place through the submicroscopic openings of the sieve plate (opening diameter 150-45Å) rather than through the sieve pores, the pressure drop across one sieve plate would be about 0.5 atm, and Weatherly (1963) has calculated that the pressure drop for flow through sieve tubes with sieve pores 0.1μ in diameter would be about 300 atm/meter of sieve tube. Observations by several investigators show a concentration gradient, which is equivalent to a pressure gradient if expressed in the

same units (atm/meter), in the sieve tube contents of approximately 0.5 atm/meter.

Concentration Gradients—Zimmerman, 1960.

Pfeiffer	0.11 to 1.04	atm/meter	var. tree species
Huber et al.	0.312	atm/meter	Red oak
Zimmerman	0.026	atm/meter	White ash

The Poiseuille equation, in its simple form, can be used to calculate the pressure drop (in atm/meter) for the flow of solution in an open tube

$$p = \frac{8\eta vl}{\pi r^4}$$

where p = the pressure difference at the two ends of the tubes in dynes per cm^2 , η = the viscosity in dyne seconds per cm^2 (poises), v = the volume in cm^3 of solution escaping per second, l = the length of the tube in cm, and r = the radius of the tube in cm (1 atm corresponds to approximately 10^6 dynes/ cm^2).

If we assume, as Weatherly has (1963), that a flow of $1\text{mm}^3/\text{hr}$ of a 10% sugar solution (Mittler, 1958) takes place in an unobstructed tube of 12μ radius, then the pressure drop should be near the observed values given above, i.e., 0.51 atm/meter. Using a 20% sugar solution a value of 0.66 atm/meter is obtained. This would suggest that the resistance of the sieve plate to flow is either very low or that the above comparison is unreal in some way. Actually the values in the above comparison are derived from different species of plants and when one remembers that there is a fourth power of the radius in the denominator of the Poiseuille equation it would appear wise to await better data before proceeding very far in this direction. The deficient points for a better understanding of pressure gradients are: pore size, tube diameter, and flow rate. The first two are usually derived from conventional measurements on "fixed" tissue: The third is derived from solution flow from a sieve tube through an aphid stylet.

It seems proper to consider the possibility of an infinite number of pumping stations, i.e., perhaps one for each sieve plate, or companion cell, along the phloem channels. This is a significant departure from the Munch system since additional forces are required—even though they may be multiple miniature forces each of sufficient magnitude to maintain the partial pressure gradient within each segment of the system. Spanner (1958) has proposed an electro-osmotic potassium pump at each sieve plate. This proposal has led to an interest in an examination of the potassium relations of the phloem, but sufficient data is not yet available to permit a decision as to whether or not this idea has merit.

Canny (1960) has measured the CO_2 evolution of the phloem and has shown a metabolic rate equivalent to the consumption of 0.5 mg of sucrose per ml of phloem per hour, or 0.012 g/day. This appears to be insufficient to operate a streaming or cyclosis mechanism (Spanner, 1962), which would appear to require 2.5 g of sucrose per ml of sieve tube sapper day. The 0.012 g may be sufficient to operate the K pumps, or some active loading system, but this is entirely speculative since the

details of such systems are lacking. The conditions of the openings in the sieve plates are, of course, the important factor controlling the amount of energy that must be expended at each plate. Spanner (1962) has discussed this matter and until some additional progress is made it seems that the selection of a mechanism for translocation on the basis of a quantitative energy requirement is improbable. One cannot even dismiss the pressure flow mechanism on the basis of energy consumption, for even the maintenance of the semipermeable membranes in the sieve-tube system is an energy-requiring process. In addition the pressure developed in a plant cell is due to an active metabolic process, the process of accumulation against a gradient.

There are a number of phenomena as yet undiscussed that are normally considered to be of importance in helping to focus on the translocation mechanism. These are: temperature, inhibitors, the log pattern, water movement, and bidirectional movement. The pressure gradient has been discussed above: Each of the others will now be surveyed in relation to mechanisms of transport.

A. Temperature

The effects of low temperature on translocation recently have been considerably clarified, in part by Ford and Peel (1966) and in part by Swanson and Geiger (1967). Both studies showed that translocation can proceed at low temperatures, i.e., -1.5°C to 2°C . An understanding of the situations controlling movement under various temperature regimes was considerably advanced by the latter authors. They found that recovery from translocation stoppage by low temperatures occurred spontaneously (without a temperature rise), and that the stoppage, in certain plants, was only a temporary condition with a predictable half life (or duration). This means that it is probably not valid to discriminate against a pressure flow mechanism on the basis of a temperature response.

B. Inhibitors

The way in which metabolic inhibitors exert their effects in controlling translocation is still in limbo. When such inhibitors are used in simple purified systems of enzyme and substrate, as in a test tube—it is possible to know their role more or less specifically. When inhibitors are applied to whole tissue their mode of producing a given effect is much more in doubt. Nevertheless, there is evidence to indicate a suppressing effect on translocation by a number of inhibitors. From this work we can state that living cells in a normal functional condition are involved in translocation, but we have known this since the earliest days of translocation research. What must be known to be relevant to a given theory of translocation is how and where the metabolic forces are applied. We can hope for more definitive data in this area as a consequence of the ever increasing knowledge of the specific roles of individual inhibitors on specific processes.

C. Log Pattern

The consequences of the log pattern of distribution of tracer in a section of phloem to the various hypotheses of translocation have been examined by Horwitz (1958) and Canny and Phillips (1963). Horwitz shows that with reasonable assumptions, both en mass flow by an osmotic pressure flow model, and certain cases of cyclosis-diffusion, can be expected to produce a log pattern of tracer distribution in the conduction system. Canny and Phillips (1963) have also shown the streaming model of Thaine to produce curves not unlike the cyclosis-diffusion curves of Horwitz. Because of the general similarity of the curves and the relatively large number of assumed parameters that are necessary in order to apply a mathematical treatment it is questionable that an interpretation in favor of a particular mechanism is possible by this means. However, this need not detract from the value of mathematical treatments, for they frequently show the possible from the impossible and they systematize and guide the creative effort.

D. Water Movement

Water movement in the phloem has been conclusively demonstrated (Biddulph and Cory, 1957; Gage and Aronoff, 1960). In dealing with this subject one must be aware of the fact that water is freely permeable through cell membranes and therefore cannot be expected to be as rigidly retained in the conduit system as is sucrose. Due to its constant exchange with indigenous water along the path of movement its front would be, and is, quickly dissipated (Gage and Aronoff, 1960). This is why very high efficiency counters such as those used by Biddulph and Cory (1957) are necessary in order to detect the front for any appreciable distance. The actual flow of the substance "water" must be considerably stronger than the measured flow of tracer water, so a demonstrated flow offers support for a general en mass flow in the sieve tubes.

E. Bidirectional Movement

The most critical single phenomenon remaining for discussion is that of bidirectional movement in the same sieve tube. This, of course, is the only sense in which bidirectional movement has significance—and it is still doubtful that it has ever been successfully demonstrated with materials normally found in plants. The experiment that appears most convincing is that of Trip and Gorham (1968) wherein tritiated sugar (glucose-6-T) was induced to move into a young leaf that had just begun to export ^{14}C -labeled sugar (from $^{14}\text{CO}_2$). The questionable aspect of this work is with the state of maturity of the leaf in whose petiole the bidirectional movement was supposed to occur. The leaf in question was apparently at the age where it could be both importing and exporting by virtue of its growth state: i.e., it was in the process of changing

over from an importing to an exporting organ, and while one portion of the leaf was still importing, another may have been exporting. This means that in closely adjacent sieve tubes there may have been monodirectional movement rather than bidirectional movement in the same sieve tube. It may also be possible that each tracer had merely distributed itself according to its own diffusion gradient (Canny and Askham, 1967). There are, however, merits to this experiment and further refinement of it using older leaves would lead to more convincing results. In our own experiments (Biddulph and Cory, 1965) we could never find the import of labeled metabolite into a leaf that was strongly exporting unlabeled metabolite—an experiment that would have disclosed bidirectional movement had it occurred. Only in the newly exporting leaf was there any suggestion of such a movement (Fig. 7-3). This indecisive period during which import continues while export begins is apparently of short duration (see above), and we have decided that during this changeover period bidirectional movement is not good evidence upon which to make or break any theory of translocation.

Kursanov (1963) has shown that the metabolite-supplying areas, the leaves, are capable of delivering sucrose into the translocation system faster than the absorbing system in the roots or fruits can remove it. The consequence is that some of it may be removed from the channel at various levels to be held in abeyance until equilibrium conditions favor its re-entry and further transport. The deposition of "half soluble" starch in cells surrounding the conducting channels has been known for many years, as has the observation that in the apple (*Malus sylvestris*) much of the reserves for flower and fruit development are stored, from the previous years photosynthate, in the twigs not many inches from the site of flower and fruit development.

It seems highly probable that the localized tissues surrounding the sieve tubes may act as a buffer system by absorbing or releasing materials—depending on their concentration in the sieve tubes and the needs of the surrounding tissues. Active absorption at any "sink" could then set in motion a flow of materials extending back along the phloem channel to the supplying leaves themselves, and if the supplying power of the leaves were insufficient to maintain normal concentrations of sucrose within the channels the reduced concentration would stimulate reloading from the temporary reserves. Weatherly et al. (1959) have shown that a pressure of sufficient magnitude to cause the exudation of phloem sap from aphid stylets can be generated in an isolated section of willow stem only 16 cm (or 800-1,000 sieve elements) in length. This indicates an internally developed pressure caused by the loading of sucrose into the sieve tubes by either the companion or parenchyma cells. The loading represents an active process that appears to be able to work against a high concentration gradient.

With an infinite number of loading stations along the channel the demands for generating large pressure differences between the two ends of the system might be circumvented, particularly if Hammel's (1968) suggestion applies—that an assimilate fluid under high pressure can move longitudinally and with less pressure drop in an inflated system, as in the phloem, than would be so if the sieve tubes were rigid.

XI. SUMMARY

In summary it should be stressed that there is, in reality, only one understandable mechanism of propulsion for translocation: This is the Münch system. All other systems (activated diffusion, streaming-cyclosis and surface active movement) are based on unknown or inadequate mechanisms as we know them and therefore require a belief that future undisclosed evidence will support them. This could occur, but for the present the pragmatic person must favor the workable hypothesis.

Yet the Münch system in its rigid form appears not to suffice. Logical modifications include a pumping system interposed along much of the conduit pathway. The pumping stations may be the potassium pumps, but anatomical evidence does not favor this. For such a system one

Fig. 7-6—The fluoresced phloem (A) and the corresponding autoradiogram (B) showing the downward component of the ^{14}C -labeled metabolite originating from the terminal leaflet of the first trifoliate leaf. The labeled metabolite is passing the cotylendnary node but the "front" of the stream is already to the root system. The movement of metabolite shows more of the characteristics of a flow pattern than a diffusion pattern.

would expect a regularity in the anatomical pattern of companion cells and sieve plates, which, in so far as I know, does not exist. The relationship appears random more than ordered. As a contributing factor for overcoming some of the resistance to passage of solute through the sieve tubes the evidence favors the loading capacities of the companion or parenchyma cells and their ability to maintain positive pressures within the sieve tubes. A further study of the Münch system to bring it into line with the additional energy required to make a workable system seems desirable. The alternate directions of attack seem toward metabolic processes, or toward a new appraisal of flow characteristics as they are related to the structural features in the living functional plant.

The most convincing visual evidence that translocation of sucrose in the plant displays a flow pattern is that of Fig. 7-6. This autoradiogram gives the distinct impression that the flow is "lead" through a specific group of sieve tubes toward a specific sink.

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7... DISCUSSION

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Two possible mechanisms: (i) Mass flow, and (ii) diffusion analogue.

Mass flow in the phloem seems to be as well substantiated as the cohesion mechanism in the xylem. The following facts seem to be well established.

A. Anatomy

Sieve tubes make up an open system of conduits. Pores through the sieve plates are 0.5 to 5.0 μ in diameter. The nucleus and most organelles are lost upon maturity. The parietal layer of cytoplasm occupies only 5% or less of the lumen.

B. Phloem Exudation

Sieve tubes comprise an inflated, elastic, open osmotic system. Initial exudation from a cut may take place at 1,000 cm/hr-10 times the normal velocity of assimilate flow. Sugar is the principal translocate. Exudation may take place for 48 hours or more from aphid stylets and the stylets tap a single sieve tube.

C. Tracer Movement

Velocities of assimilate movement have been recorded up to 360 cm/hour. Distribution follows a source-to-sink pattern. Mature leaves are bypassed. Toxic and nontoxic compounds assume similar patterns and they go where the sugar goes.

D. Calculations

Using the Poiseuille equation the following resistances to flow through sieve tubes and sieve plate pores have been calculated. They indicate that the mass flow mechanism may very well account for assimilate translocation in plants.

Calculations*	Cucurbits	Willow	Pine
Sieve pores	0.38	0.32	0.48
Open tubes	0.05	0.23	0.07
Total	0.43	0.55	0.55

* Resistances thru sieve pores in atmospheres per meter.

Cucurbits (*Cucumis* sp.; *Citrullus* sp.; *Cucurbita* sp.)—For a 15% sucrose solution having 12 atm osmotic pressure (OP) flow could occur through 28 or 92 feet.

Ash (*Fraxinus* sp.)—For ash gravity would account for 0.1 atm per meter, and with an OP of 12 atm, would transport against a resistance of 0.33 atm/meter and would allow for a flow through 37 or 122 feet.

Willow (*Salix* sp.)—For a 12.5% sucrose solution having 10 atm OP, flow could take place against a resistance of 0.45 atm/meter through 22 m = 74 feet.

Pine (*Pinus* sp.)—For a 25% sucrose solution having 25 atm OP, flow could take place through 56 m equivalent to 185 feet.

In all cases cited for trees the lower branches could well be below the above heights.

E. Alternatives

1) There are no pistons, no valves, no impellers in the sieve tubes. What sort of pumps could possibly serve to move the assimilate stream?

2) Volume relationships—the cytoplasm occupies 5% or less of the total lumen volume of the sieve tube whereas sugar may occupy 10 to 15% more. If cytoplasm provides the surface or makes up the pumps they would have to move 2 to 3 times their own volume at 100 cm/hour.

3) The pumping mechanism would have to handle 2,4-D, amitrole, 2,3,6 TBA, picloram, MH, endothall, fenac, amiben, dalapon and other toxic materials. It is difficult to visualize metabolic pumps that would do this.

4) The pattern of distribution of these toxic substances is not random, as by diffusion. They all go where sugars go as along in a stream, accumulating in meristematic regions (shoot and root tips) and bypassing mature, exporting leaves.

7...DISCUSSION

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Although the weight of evidence continues for the most part to favor the pressure-flow hypothesis, I will speak briefly on recent unpublished observations made in my laboratory which are not readily compatible with this view.

Earlier we showed in sugar beet (*Plant Physiol.* 42:751-756, 1967) that the rate of sucrose translocation from a mature leaf to a rapidly expanding leaf is only temporarily inhibited by chilling a 2-cm zone of the donor-leaf petiole to 1-2°C. These studies have since been repeated at 0°C with essentially the same results. After about 2 hours, the rate of translocation across the chilled zone is restored to the pretreatment rate, even though the petiole zone is maintained at 0°C.

Assuming that the chilled zone imposes an increased resistance in the translocation system (as a result of radial contraction of the sieve tubes, increased viscosity of water, callose formation, decreased rates of oxido-reduction processes which presumably maintain electrical gradients across sieve plates and membranes, etc.), it may be postulated that the observed homeostasis in translocation rates is effected through corresponding adjustments in pressure gradients across the 0°-zone.

This hypothesis predicts that the equilibrium pressure gradient across an 8-cm 0°-zone should be four times the pressure gradient across a 2-cm 0°-zone. It may be anticipated, therefore, that the kinetics of the homeostatic process under these two conditions would be different. However, a careful comparison of the recovery times for translocation rates across the 2-cm and 8-cm 0°-zones revealed no sensible differences. Similarly, measurements of the sucrose concentration gradient in the petioles under these two conditions were not significantly different. These data suggest that higher pressure gradients are not required to maintain a constant rate of translocation across zones of higher flow resistance, and hence are in violation of the simple Poiseuille relationships required by the pressure-flow hypothesis.

The required experiment to make this conclusion more convincing is to measure simultaneously changes in the hydraulic pressure drop across the chilled zone and changes in the translocation rate. Conceivably this can be done by measuring the relative exudation rates from aphid stylets implanted above and below the chilled zone and relating the time course in relative rates of exudation at these two sites to the time course in translocation rates. Independent variations in these parameters would invalidate the pressure-flow hypothesis. We plan to continue further studies along these lines.

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