MOVEMENT OF ORGANIC MATERIALS IN PLANTS: A NOTE ON A RECENTLY SUGGESTED MECHANISM[1]

F. C. STEWARD AND J. H. PRIESTLEY

A recent paper by CRAFTS (1) discusses in an interesting manner the mechanism which effects rapid movement of organic solutes in the tissues external to the cambium. That such rapid movement, usually in a downward direction, does actually occur few will question. The general magnitude of sugar and also of organic nitrogen movement has been estimated by MASON and MASKELL to be of the order of physical diffusion in gaseous systems rather than the much lower rates, possible by diffusion alone in aqueous systems. Such a problem clearly demands careful scrutiny of any theory regarding a possible physical mechanism, especially one elaborated with due regard to the histological nature of the tissues concerned. CRAFTS suggests a mechanism very similar to that of MÜNCH (3) but is led by certain interesting anatomical observations to suggest that the translocation proceeds not in the sieve tubes (the most striking, longitudinally specialized cells of the phloem) but principally along the cell walls of the whole phloem tissues including sieve tubes, companion cells and parenchyma. The mechanism is not analogous to diffusion as MASON and MASKELL propose but is definitely dependent upon mass flow of solution in the cell walls. CRAFTS develops his theory as the result of a laudable attempt to decide anatomically the route offering least resistance to mass flow. The writers have every sympathy with such an anatomical approach but are equally clear that any apparent conclusions indicated on purely anatomical grounds must be interpreted strictly in accordance with physical principles and probability. We welcome the interesting contributions which CRAFTS has made to the histology of the phloem but it is the purpose of this note to show that some of the interpretations fundamental to the mechanism suggested are physically inadmissible.

CRAFTS' rejection of the sieve tubes as the path for translocation in favor of the cell walls is a distinctly novel feature. This follows principally upon the interesting observation that the total cross-sectional area of the phloem mounted fresh is composed of cell wall material in much greater degree than would be expected from preparations fixed and mounted in the usual manner. In the latter case it is shown that marked shrinkage of the wall occurs. The relative contributions of sieve tubes, pores in sieve plates, and the walls of all the phloem cells to the cross-sectional area of undried phloem were estimated by projection methods. CRAFTS arrives at the con-

[1] From the Department of Botany, University of Leeds, England.

clusion that, with due regard to the total area of sieve tubes, the presence of frequent sieve plates with small pores, and the hitherto unsuspected area of wall substance, the latter route would be the more efficient. This conclusion is justified on two principal grounds: (1) The calculated pressure gradient required to transmit a probable sugar solution by mass flow along the sieve tubes at a rate sufficient to ensure the observed transfer of dry matter (a) along a potato stolon, (b) in the stem of *Cucurbita,* (c) out of a leaf, are large (of the order of 20 atmospheres per meter). Similar calculations indicate that the corresponding pressure gradients necessary to effect transfer along the cell walls of the phloem are quite small (of the order of 1×10^{-6} or 6×10^{-5} atm. per cm. and actually as low as 1.6×10^{-8} atm. per cm. to secure transfer in a tree). (2) It is suggested that exudation studies on cut phloem tissues indicate normal mass flow in the walls of the phloem of an order quite adequate to secure the observed transfer of organic nutrients.

The most important argument is that based on the required pressure gradients along the sieve tube and walls respectively. The necessary calculations were based on the familiar Poiseuille relation between the rate of flow and the pressure gradient along a tube of uniform cross-section, the viscosity of the solution, and the dimensions of the tube under conditions of uniform, non-turbulent flow. It is the purpose of the writers to show that the use made of the Poiseuille relation is such as to arrive at quite incorrect conclusions. CRAFTS arrives by a rather devious series of calculations at a figure for the pressure necessary to cause a mass flow at the required rate through the sieve pores of *Cucurbita.* In spite of the fact that the formula used is for uniform horizontal flow through a capillary this figure no doubt represents the order of pressure gradient required (20 atmospheres per metre). However, it is compared with a pressure calculated to represent that necessary to cause a mass flow at the required rate along the walls of the total phloem. It may be stated definitely that this pressure (1.5×10^{-5} atmospheres per cm.) has no relation whatsoever to the true pressure involved. The reason is fairly obvious. In this, as in all other cases where CRAFTS calculates pressure gradients necessary to cause mass flow along walls, he treats the total phloem wall area (or in the case of *Cucurbita* the wall area per bicollateral bundle) as a single pore. By various means this (the total wall area) was derived, and the radius of the equivalent circular area determined (see p. 18 and also p. 14, etc.). This radius was then inserted in the Poiseuille relation in which r can legitimately equal only the radius of a single capillary, thus:— $P = \frac{8Rnl}{\pi r^4}$.

where
- P = pressure in dynes per sq. cm.
- R = rate of flow in cc. per sec. through total phloem walls.
- n = viscosity of a 10 per cent. sugar solution.
- l = length of gradient or tube in cm.
- r = radius of conducting element due to the walls of which the shearing forces are exerted.
- A = area of capillary through which flow takes place.
- R_1 = linear rate of flow.

After CRAFTS:

$$R = R_1 \times A$$

$$P = \frac{8R_1 \times A \times n \times l}{\pi r^4}$$

$$P = \frac{8R_1 \times \pi r^2 \times n \times l}{\pi r^4}$$

$$P = \frac{8R_1 nl}{r^2}$$

where r = radius of circle equivalent to total phloem wall.

Correct:

$$R = R_1 \times A \times N \qquad A = \pi r_1^2$$

$$P = \frac{8R_1 \times A \times n \times l \times N}{\pi r_1^4}$$

$$P = \frac{8R_1 \times \pi r_1^2 \times n \times l \times N}{\pi r_1^4}$$

$$P = \frac{8R_1 \times N \times n \times l}{r_1^2}$$

where r_1 = radius of a single, circular, conducting element.
N = number of such capillaries in total area through which flow proceeds.

The resistance to flow through small pores depends on the shearing forces which are the result of steep velocity gradients in the moving liquid. The liquid in contact with the pore wall is theoretically at rest and that farthest from it has maximum velocity. In the Poiseuille expression for steady flow through a horizontal uniform circular capillary r represents the distance separating liquid surfaces at rest from that moving with maximum velocity. By utilizing in Poiseuille's expression the radius of the circular area equivalent to the total phloem area and a derived linear rate of flow, CRAFTS in effect says that the theoretical liquid surface at rest in contact with the pore wall is separated from that of maximum velocity by a relatively large length—the radius of the circle equivalent in area to the total phloem wall—whereas if flow did take place through the walls, it is clear that the true value should be of the order of half the mean wall thickness. In short, CRAFTS found the radius of the *actual pores* through the sieve plate, but when dealing with flow through the whole wall used a pore radius of a wrong order of magnitude. Since the formula demands $\frac{1}{r}$ to the fourth power it is clear that the derived pressures are of a totally wrong order of magnitude.

From the preceding formulae it is seen that one ought to multiply CRAFTS' derived pressures for mass flow through walls by a quantity $\frac{r^4}{r_1^4}$, since N obviously $= \frac{\pi r^2}{\pi r_1^2}$. This factor which equals the $\left(\frac{\text{radius of the equivalent single pore}}{\text{radius of the true, circular capillary pore}}\right)^4$ is large. If flow assumed through the whole wall is to be calculated as through circular pores at all,

it would seem legitimate to state that r_1 at its maximum must be of the order of half the mean wall thickness. From CRAFTS' projection figures and magnification factors this can be estimated and r is known. It is thus possible to show that, whereas CRAFTS calculated that very small pressures would be adequate to cause the required mass flow along walls these are really of the general order of 10^6 times too small. For example, in the case of the potato stolon the value of 1.1×10^{-6} atmospheres per cm. is more probably of the order of 78.2 atmospheres per cm. Similarly the small pressure gradient of 1.5×10^{-5} atmospheres per cm. calculated as necessary to cause adequate mass flow through the walls of the phloem of *Cucurbita* becomes 11.89 atmospheres per cm. The same argument applies to all the pressure gradients calculated for flow through phloem walls. The bigger the area of the single pore used by CRAFTS (*i.e.*, the area of total phloem wall) the more improbable do his pressure gradients become. It will be noted that these more probable pressures assuming flow through the whole wall are either numerically greater than, or of the same order of magnitude as, those estimated to secure mass flow through the sieve pores. The conclusion, therefore, that the pressure gradients necessary to secure flow through walls are much less than those required to cause mass flow through the sieve pores, is on these grounds alone unsound. It is true that CRAFTS does not suggest that the total phloem wall is really a single pore, but he regards the factor of 4400 which represents the discrepancy between his derived pressure and that gradient which he conceives to be probable, as sufficient safeguard against the "walls acting as a single capillary and acting as they do in the plant"—(*l.c.*, p. 20).

It is clearly unsatisfactory to use the expression for flow through circular pores at all. The exact calculation for flow along a system of the type of the phloem wall would be difficult to compute. One can, however, estimate the pressure gradients necessary to cause the required mass flow along the phloem wall were this straightened out to form a single sheet bounded by parallel plane surfaces separated by the mean wall thickness. For uniform viscous flow of a liquid of viscosity (n) between parallel planes, the pressure gradient per cm. $\left(\frac{dp}{dy}\right)$ is given in terms of the volume rate of flow per sec. (V) across unit width (h sq. cm.) between planes h cm. apart by the formula (2): $V = -\frac{h^3}{12n} \times \frac{dp}{dy}$ $\qquad V = Uh$ where U = linear rate of flow.

$$U = -\frac{h^2}{12n} \times \frac{dp}{dy}$$

For the case of *Cucurbita* (p. 18) using U = 0.0759 cm. per sec. (not 0.045 as CRAFTS[2] calculates)

[2] CRAFTS derives the mean linear rate by dividing the mean of a series of total flows by the mean of a series of areas. He ought to work out the linear rates individually and find the mean of these. (See top, p. 16.)

$$h = \frac{0.25}{400} \text{cm. estimated from Plate Va}$$

$$n = 0.015$$

$$\frac{\partial p}{\partial y} = 3.50 \times 10^4 \text{ dynes per sq. cm. per cm. length}$$

$$= 0.035 \text{ atm. per cm. approximately.}$$

Pressure gradient per metre = 3.50 atm. approximately.

This value, which assumes in effect that the moving liquid is only sheared in a direction at right angles to the wall surface, is perhaps a minimum one and is of an entirely different order of magnitude from that calculated by CRAFTS. Further analysis of the application of the Poiseuille expression to mass flow of solution through the whole of the phloem walls seems superfluous since it is obvious that the whole wall cannot admit of mass flow. The actual pores are probably sub-microscopic and of the order of intermicellar spaces, *i.e.*, quantities to be measured in Ångström units. Without attempting further computation it is obvious that with this in mind even the preceding pressure gradients themselves of the order of 10^6 times those utilized by CRAFTS to support his thesis are really much too small. It is clear that CRAFTS himself realizes this point for in his discussion he says: "The fact remains that the spaces through which it is proposed that food materials in solution are passing are of molecular dimensions and irregular in form. Since no formulae are available by which to calculate pressure gradients and rates of flow through this type of material mathematical treatment is impossible. Use of Poiseuille's formula leads to high values fully as great as the ones which appeared on the sieve tube calculations."

In spite of this the whole case that the actual flow is through the walls depends for its justification upon the pores through which the flow takes place being not only much greater than the visible sieve plate pores but actually greater than the wall thickness itself. The probable pressures to secure mass flow through the whole wall are certainly either of the order of, or greater than, those calculated for flow through the sieve pores whose actual diameter was computed. From the molecular constitution of the cell wall as now known the presumption is that a mass flow could proceed more readily through the sieve tubes with their visible pores than along the phloem walls.

Since the application of the Poiseuille expression to the mass flow of solution along the phloem does not really justify the conclusion (as CRAFTS claimed) that the movement of organic solutes is along the walls, is there other evidence which does support such a novel idea? CRAFTS utilizes the well-known fact that the phloem of *Cucurbita* exudes droplets of sap as evidence of normally occurring mass flow in the phloem. From measurements of total phloem wall and also of sieve tube and sieve pore areas in

the plants concerned he concludes by arguments identical with those already criticized that this flow takes place in the walls and not in the sieve tubes. We wish, however, to draw attention to the data which indicate that the rate of such flow, as determined by exudation studies, would be adequate to effect translocation into cucurbit fruits. The linear rate of flow presumed to be in the phloem walls was determined from the volumes collected in a given time. However, the flow was never observed for a period *longer than five minutes.* Where consecutive collections were made from one stem after a single cutting, the rate observed steadily decreased with time and stopped after five or six minutes (see table VII). In fact to make several collections from a single stem it was necessary to cut the stem repeatedly. This is ascribed to plugging of the cut surface by proteinaceous material which gelatinizes upon exposure to air. It seems much more probable that in a succulent plant of the type used the exudation from the phloem is not an indication of a normally occurring mass flow at all, either in the walls or sieve tubes, but may be due rather to the turgor of surrounding tissues and the release of tissue tensions consequent upon cutting. A new cut then merely opens up a new length of stem. However, apart from such a criticism, drastic as it is, CRAFTS is surely not warranted in comparing the rate of flow in cm. per min. observed over a period *not exceeding five minutes during which constant values were never attained* with the rate of flow calculated as necessary to account for uptake of dry matter by a pumpkin. In the latter case the rate is assumed uniform *over a period of 100 days* and the rate is calculated as cm. per min. Allowing such latitude in the choice of time intervals and such tolerance of what constitutes a steady flow can produce only purely fortuitous arithmetical agreement of results.

It is not our purpose to discuss the basic principle of the mechanism suggested by MÜNCH and CRAFTS, interesting as it is. We merely wish to point out that whether or not the phloem walls do form an important avenue for translocation, the data and argument used by CRAFTS to arrive at this conclusion are unsatisfactory, and ought logically to lead to a different one. The interesting fact remains that phloem *in vivo* has apparently much thicker, hydrated walls than we have hitherto supposed. That, however, does not necessarily indicate that they function in translocation over long distances. The application of formulae from classical physics, which apply usually to well defined cases which are rarely, if ever, satisfactorily duplicated in the living plant, involves often the adoption of arbitrary assumptions which may vitiate the conclusions drawn. We feel that in this particular case the utilization of the Poiseuille relation is particularly unfortunate and has led to entirely erroneous conclusions.

DEPARTMENT OF BOTANY,
UNIVERSITY OF LEEDS.

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