SHORT COMMUNICATIONS

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Evidence for the electroosmosis theory of transport in the phloem

The electroosmosis theory of phloem translocation was put forward by FENSOM[1] and SPANNER[2]. It has the attraction of linking evidence that sugar moves in the sieve tubes in solution by mass flow[3] with the high physiological activity of phloem[4].

The theory as envisaged by SPANNER[2] requires three conditions for electroosmosis to occur across the sieve plates in the phloem. They are: (a) an electrical potential gradient across the sieve plate; (b) a secretion of K^+ into the sieve tube on one side of the sieve plate and a corresponding removal of K^+ on the other side; (c) the potential difference across each of the sieve plates in an individual sieve tube must be polarised in the same direction.

Evidence for each of these conditions has now been obtained from the primary phloem of the vine (*Vitis vinifera*) and is described below.

TABLE I

THE POTENTIALS (mV) OF ADJACENT SIEVE ELEMENTS WITH RESPECT TO THE BATHING MEDIUM AND THE POTENTIAL DIFFERENCE ACROSS THE INTERVENING SIEVE PLATE

Bathing medium, 0.25 M sucrose + 1 mM KCl. Measurements from 10 sieve tubes in the primary phloem of vine (*V. vinifera*). (*a*) is the sieve element with the more negative potential in each case.

	Sieve element		*Potential difference across intervening sieve plate*
	(*a*)	(*b*)	(*a* − *b*)
	−47	− 4	43
	−40	−26	14
	−20	− 3	17
	−22	− 5	17
	−19	− 2	17
	−25	− 4	21
	−23	−12	11
	−43	− 9	34
	−32	−25	7
	−31	−25	6
Mean	−30	−11	19

The results of measurements of the potential difference across the sieve plate of Vitis obtained during the summer of 1967 have already been reported[5]. The results of determinations made during July and August 1968 are shown in Table I. They were obtained by measuring the potentials of adjacent sieve elements with respect to the bathing solution (0.25 M sucrose + 1 mM KCl) using calomel microelectrodes as described previously[5]. The potential difference across the intervening sieve plate was taken as the difference between each pair of values.

The mean value in Table I of the potential difference across the sieve plate (19 mV) agrees closely with that for the previous determinations in which the potential was measured directly (also 19 mV)[5].

The chemical activity of potassium in Vitis phloem was determined as follows: A length of stem was cut from the current year's growth and the bark peeled away from the wood at one end. A 1-μl Microcap pipette was placed over the cut end of the bark in the region of the phloem. Approx. 0.1–0.5 μl of clear sap was drawn into the tube by capillary action. This was assumed to be sieve tube sap although it may have also contained sap from the other cells of the phloem. The small samples were transferred to a coverslip which was then inverted over a moist chamber on a microscope stage. The K^+ activity was determined by inserting a potassium-specific microelectrode (tip diameter 1 μ) into the drop of sap. This electrode, developed by James Dunlop in this Department, is approx. 700 × more sensitive to K^+ than to Na^+. The range of values obtained was 89–100 mM with a mean value of 94 mM. This lies between the values obtained by TAMMES[6] and PEEL AND WEATHERLEY[7].

Knowing therefore the electrical potential (E) between the outside and inside of the cell and the K^+ activity inside and outside, the direction and magnitude of the gradient of electrochemical potential for K^+ ($\Delta\bar{\mu}_K$) can be calculated from the following equation:

$$\Delta\bar{\mu}_K = zF(E-E_K)$$

Where z = valency of K^+, F = the Faraday constant, E = observed potential (V) and E_K = the Nernst potential for K^+ (V).

Substituting either of the two values for E in Table I into the above equation we find that potassium is being held in the sieve tube against an electrochemical potential gradient. The potassium concentration must be maintained by metabolic energy, or in other words, we have evidence for an inwardly directed potassium pump. Furthermore, the driving force tending to drive K^+ into the sieve tube is greater on the more positive side of the sieve plate (2422 cal·mole^{-1}) than on the more negative side (1960 cal·mole^{-1}) and this will cause a flow of K^+ across the sieve plate towards the negative side. Presumably the potassium pumps are sited in the plasmalemma lining the longitudinal wall of the sieve tube since the tonoplast disappears early in the development of the sieve cells[8].

If the potential difference across each sieve plate in a sieve tube is polarised in the same direction the sharp change of potential at each sieve plate must be negated by a more gradual decline in potential along each intervening sieve element, resulting in a "saw tooth" pattern of potential. The alternative to this "saw tooth" pattern is a "square wave" condition with alternate sieve elements having uniformly low or high negative potentials. In this condition the sieve plate potentials at opposite ends of each sieve element would be in opposite directions tending to cancel each other out and long distance transport due to electroosmosis would not occur.

The simplest way to try to detect a decline in potential along the sieve element would be to insert a microelectrode at each end. This unfortunately was not possible at the microscope magnifications used (800×) for only part of the sieve element (length approx. 250 μ) was in the field of view. Instead, one electrode was inserted at one end, withdrawn, and re-inserted at the other end of the sieve element. This technique suffers from the objection that withdrawal from the first position may

result in a decline in potential difference between the inside and outside of the cell due to the failure of the membrane to completely reseal itself which would cause the second reading to be erroneously low. It was thought, however, that if the second determination in the same sieve element was found to be greater than the first, such a loss of potential, if it occurred, would not materially affect the interpretation of the results.

Fig. 1 shows the results obtained from 4 contiguous sieve elements in two different sieve tubes. In these measurements the lower value in each sieve element was obtained first. Other similar results were obtained in which the higher value was

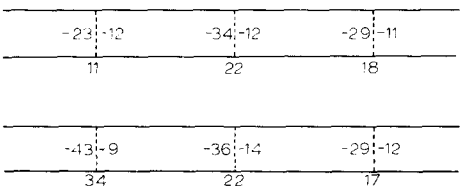

Fig. 1. The trend in potential, with respect to the bathing solution, in neighbouring sieve elements from two sieve tubes of Vitis and the potential differences across the intervening sieve plates (mV). The microelectrode was inserted approx. 10 μ from the sieve plate for each determination of potential difference.

obtained first. It can be seen from Fig. 1 that the potential differences across each of the sieve plates in the same sieve tube were found to be polarised in the same direction. The mean value of the potential differences across the 6 sieve plates in Fig. 1 is 19 mV which agrees with the mean value in Table I and with the results previously published[5]. A decline in potential difference due to the technique therefore does not appear to have occurred.

It must be emphasised that these results were obtained with isolated sections of phloem and the potentials could be artifacts developed as a result of the cutting of the tissue although there is no evidence that potentials measured in other plant tissues are artifacts due to the treatment of the material. However, bearing this in mind, these results do suggest that electroosmosis could be the underlying mechanism of phloem translocation.

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