THE MASS-FLOW THEORY OF PHLOEM TRANSPORT; A SUPPORTING CALCULATION

by

L.K.WIERSUM

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The Mass-flow Theory of Phloem Transport; A Supporting Calculation

L. K. WIERSUM

Institute for Soil Fertility, Groningen

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THE mechanism of long-distance transport in the phloem has not been definitely elucidated. Although the hypothesis that the transport of solutes is brought about by mass-flow has many adherents, it is still criticized and contested. In our own experiments on Ca-transport in relation to physiological disorders, the results could be well explained by accepting the occurrence of a flow of water carrying the solutes in the phloem (Wiersum, 1966).

Recently in a paper published by Hagemann (1964) the distribution and redistribution of mineral nutrients in the potato have been closely followed. The most interesting data are given in Table 1, where the mineral content, dry matter, and fresh weight of the seed-potato are followed at weekly intervals during the development of the young sprout. The decrease of dry matter, potassium, phosphate, and magnesium in the seed-potato during sprouting is ascribed to export in the phloem. During this process, however, the total amount of Ca in the seed-potato increases, which phenomenon Hagemann relates to uptake via the xylem from the roots.

TABLE 1 (Hagemann, 1964)

Fresh weight, dry weight, and mineral content of the sprouting tuber (excluding sprouts)

Weeks after planting	Fresh weight in g	Dry weight in g	Mineral content in mg per tuber			
			K_2O	P_2O_5	CaO	MgO
0	59·8	17·78	345	99·6	10·7	24·9
3	71·1	13·56	245	74·6	32·5	23·1
4	69·9	9·22	166	51·6	46·1	23·1
5	68·3	6·41	114	32·7	59·6	23·7
6	66·4	5·29	79	23·8	65·6	22·7
7	68·0	4·03	66	17·7	68·5	24·2
8	60·7	3·27	48	13·7	71·0	23·9
9*	46·8	2·79	37	11·2	73·1	24·0
10*	43·8	2·37	25	8·1	67·1	23·0
12*	31·9	1·86	25	5·8	70·1	21·6

* These data have not been used because of deterioration of tubers.

The sprouting seed-potato is thus a unit importing water and minerals and exporting organic material and most of the mineral stock. The exceptional behaviour of Ca, an element hardly transported in measurable amounts in the phloem, gives the opportunity to estimate the total water balance of the tuber.

For this purpose the validity of the mass-flow theory is accepted. Some simplifications have to be made, of which the most important is that the influx of water from the roots is considered to transport negligible amounts of potassium and phosphate.

In the first 3 weeks the amount of water in the tuber has risen from $59{\cdot}8-17{\cdot}8 = 42{\cdot}0$ to $71{\cdot}1-13{\cdot}6 = 57{\cdot}5$ g, an increase of 15·5 ml. The export of organic matter and minerals will, however, also have necessitated an extra supply, which is consumed in the outflow over the sieve tubes. This unknown amount is provisionally designated as A. This A ml water has transported $99{\cdot}6-74{\cdot}6 = 25{\cdot}0$ mg P_2O_5 to the sprout. The total influx of water to the tuber in the first 3 weeks has thus been $15{\cdot}5+A$ ml, an amount which imported the increase in CaO amounting to 21·8 mg.

After 4 weeks the amount of water in the tuber has increased by 18·7 ml. The amount of water used for export is considered to be proportional to the decrease in phosphate and can thus be set at $48/25\times A$ ml. Thus the total amount of water imported must have been $18{\cdot}7+(48/25)A$ ml, carrying $46{\cdot}1-10{\cdot}7 = 35{\cdot}4$ mg calcium. Assuming a constant level of calcium in the entering xylem sap the following equation can be written:

$$\frac{15{\cdot}5+A}{21{\cdot}8} = \frac{18{\cdot}7+(48/25)A}{35{\cdot}4}.$$

Solving the equation gives $A = 22$ ml.

If we further assume that the water exported in the phloem is proportional to the export of phosphate during the next weeks, the total water balance of the tuber can be estimated. The amounts calculated on these assumptions along with the amounts derived from the original data are set out in Table 2. The nearly constant calcium concentrations in the entering xylem sap, as estimated in this manner, point to the validity of the approach. It can also be seen that the increase in CaO is related to the amounts of phosphate and K_2O exported.

In the course of 8 weeks the calculated efflux of water is

$$\frac{99{\cdot}6-13{\cdot}7}{99{\cdot}6-74{\cdot}6}\times A \text{ ml} = 3{\cdot}44\times 22 \text{ ml} = 75{\cdot}7 \text{ ml}.$$

This amount of water has carried 14·5 g dry matter (mainly sugars), approximately 300 mg K_2O and about 86 mg P_2O_5. The composition of the solution flowing through the phloem can thus be calculated. The result is given in Table 3, which also contains for comparison the data obtained on the phloem exudate of *Yucca* (Tammes and van Die, 1964). The estimation shows that the calculated composition bears a resemblance to the analytical data.

The calculated concentration of CaO in the inflowing xylem sap shows a rather constant value, which would be more or less expected. The concentration is also a very reasonable one, and is comparable to that of 0·346 and 0·99 mg/ml as found by Schardakoff (l.c. Arisz, 1942) in analysing xylem exudate from *Papaver* and *Brassica*, and of 0·38 mg/ml as found by Moore, Mason, and Maas (1965), as maximum value.

The same phenomenon of Ca accumulation during depletion of a storage organ has been observed by Klein (1965) during germination of corn seeds.

The results obtained in this rather crude calculation in which secondary effects have been neglected, clearly support the validity of the hypothesis that it is a mass flow of water in the phloem which carries out the substances exported from the tuber.

TABLE 2

Derived data, in italics, and estimated amounts of influx and efflux of substances in the sprouting tuber

Weeks from planting	Water balance of the tuber in ml: Nett. H_2O increase	Total influx	Phloem efflux	Loss of P_2O_5 (efflux)	Loss of K_2O (efflux)	Increase of CaO in mg	Concentration of CaO in influx in mg/ml
0	..	..	..	..			
3	*15·5*	37·5	22	*25·0*	*100*	*21·8*	0·58
4	*18·7*	60·9	42·2	*48·0*	*179*	*35·4*	0·58
5	*19·9*	78·0	59·0	*66·9*	*231*	*48·9*	0·63
6	*19·1*	85·1	66·0	*75·8*	*266*	*54·9*	0·64
7	*22·0*	94·2	72·2	*81·9*	*279*	*57·8*	0·61
8	*15·4*	91·1	75·7	*85·9*	*297*	*60·3*	0·66

TABLE 3

Comparison of calculated data on the composition of phloem sap and data obtained by analysis (Tammes and van Die, 1964)

	Results expressed in mg/ml: Dry matter	K	P
Estimated	192	3·2	0·5
Analysis	185	1·68	0·31

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