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Phloem Pressure Differences and ^{14}C-Assimilate Translocation in *Ecballium elaterium*[1, 2]

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ABSTRACT

The role of phloem turgor pressure in ^{14}C-assimilate translocation in *Ecballium elaterium* A. Rich was studied. The direction of translocation was manipulated by two methods: darkening, or defoliation, of the upper or lower halves of the shoots. After 24 hours of labeled assimilate movement, sieve tube turgor levels were measured with the phloem needle technique. Distribution of label, determined by autoradiography and counting, revealed a direct correlation between the direction of assimilate transport and the pressure difference. Phloem turgor levels always decreased in the stem of darkened shoots; this resulted in greater pressure differences in the stem between the source leaf receiving $^{14}CO_2$ and treated regions.

Opinions have been divided for a long time as to the mechanism of phloem translocation. Most plant physiologists agree that there is a mass flow of sieve tube sap, solutes, and water moving as a stream through mature sieve tubes. This flow is thought to be "powered" by turgor gradients which are osmotically produced (2, 17). The pressure flow mechanism is supported by abundant evidence obtained from studies of sieve tube exudation (2, 20, 21, 26, 28, 29); movement of viruses (5, 6), dyes (1, 3, 7, 8, 21), ^{14}C-assimilates, and plant regulators (4, 16, 27). Although the importance of pressure gradients is minimized by some workers (9, 25), the general view is that a pressure difference between source and sink is essential for phloem conduction.

Little has been done in the way of direct measurement of turgor gradients in sieve tubes. Hammel (13) provided direct evidence of relatively high phloem pressure in the source region of *Quercus rubrum* by using the "phloem needle," but there is an obvious need for more quantitative data, using plants grown under controlled conditions.

The objective of the present study was to measure the phloem turgor pressure in different parts of the plant and to determine the relation of pressure differences to ^{14}C-assimilate movement in this tissue.

MATERIALS AND METHODS

Plant Material. Squirting cucumber (*Ecballium elaterium* A. Rich) seedlings were grown under greenhouse conditions until they were 35 to 40 cm tall. They were then transferred to a growth chamber providing a 16-hr light period (2,400 ft-c) and temperature of 28 C. Twenty four hr before application of $^{14}CO_2$, depending on the particular experiment, the upper or lower half of the shoot was defoliated, or darkened with three layers of paper bags or aluminum foil to prevent photosynthesis. Air was circulated within the bags or foil coverings to prevent CO_2 accumulation. The bags and covers were removed 24 hr after ^{14}C application, just before the phloem pressure measurements.

Phloem Needle Technique. The phloem needle assembly was identical to that devised and used by Hammel (13). It consisted of a modified 26-gauge hypodermic needle with two holes on opposite sides of the tip. A brass fitting with a hole in the middle served as a handle. This was slipped over the needle and soldered, leaving about 1 cm of the needle tip free. The base of the needle was connected to a glass capillary by means of a short length of polyethylene tubing. The needle, connector, and half of the capillary were filled with air-free distilled H_2O containing 0.01% (w/v) methylene blue. An air column of 15 to 20 cm remained and the end of the capillary was sealed in a flame. Each phloem needle was calibrated with an adjustable source of pressure.

Phloem pressure measurements were made by slowly pushing the needle into the stem to a depth of about 2 to 3 mm. On penetration of a phloem bundle by the needle tip, the air column in the capillary was instantaneously compressed by a surge of the dye solution. The pressure value was obtained by reading the length of the compressed air column and referring to the calibration curve. Further technical details can be found in Hammel's paper (13). Not all measurements were successful, but in the majority of attempts, positive readings were obtained. Occasionally a test failed because the inner or outer phloem of the bundle was missed, or because the needle tip was blocked. Usually the needle entered the external phloem. A rapid compression of the air column was considered to indicate a good reading, and only these readings were included in the data.

Tracer Experiments and Turgor Measurements. Radioactive CO_2 was prepared from ^{14}C-sodium bicarbonate solution and applied to a mature leaf attached to a median node. Approximately half of the leaf (apical portion) was enclosed tightly in a chamber having light weight plastic windows 6.2 × 7.5 cm in size, and a sponge rubber frame. A 10-ml aliquot of air containing 40 μCi was drawn from a generator bottle with a syringe and injected into the chamber through the rubber sealing edge. Treated leaves were allowed 10 min for $^{14}CO_2$ fixation in sunlight (outdoors); the amount of ^{14}C fixed was in the order of 1 μCi. The chambers were then removed and the plants were transferred to the growth chamber.

After 24 hr of translocation, sieve tube turgor was measured with the phloem needle at three stem locations: P_1 at the top of the shoot, about 1.5 to 2 cm from the apex; P_2 at the node of the treated leaf; and P_3 at the lower part of the shoot, about 2 cm from the soil line. There were two measurements in each loca-

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tion and the sequence of needle penetration at the three locations was random.

The turgor difference between the median portion of the stem ("source region") and the upper and lower stem regions was obtained by calculating the values of $P_2 - P_1$ and $P_2 - P_3$. In order to show the difference in pressure gradients between the upper and lower stem regions, the value of $(P_2 - P_1) - (P_2 - P_3)$ was calculated. Mean ± SE was calculated for each experiment.

Translocation was terminated by quickly dividing each plant into seven portions for radioactivity counting: two parts above the treated leaf (leaves, stem), treated leaf, and four parts below (leaves, stem, fleshy root, fibrous roots). These portions were dried at 80 C for 48 hr, and after total dry weight determination, they were ground in a Wiley mill. Thirty-mg samples were counted twice, 10 min each, in a Nuclear-Chicago model 1042 counter. Net counts less than 5% of background were considered zero. The percentages of radioactivity in the two parts above the treated leaf and also in the four parts below the treated leaf were added to obtain the total amount of ^{14}C translocated.

The amounts of ^{14}C-assimilate translocation, expressed as a percentage of the sum of cpm in all of the regions, were evaluated by the one-way analysis of variance method (10). The difference between the percentage of radioactive distribution in two regions, above and below the treated leaf, was calculated. The means of the differences in the percentage of radioactivity were calculated for each treated and control plant, with six replications of the treated and two or four replications of the controls.

In addition to counting, several cross-sections of stem 1 to 2 mm thick, small portions of leaves 2 to 3 cm^2 in area, and a sample of the root, including cross-sections of the large fleshy root and some of the fibrous roots, were randomly cut from the seven portions of each plant. These samples were taken from different heights and were mounted in order on white paper for autoradiography. Each sheet was put between two blotters and dried at 38 C for 48 hr. They were then exposed to x-ray film for 30 days.

The relation between changes in phloem pressure and $^{14}CO_2$-assimilate translocation was studied in four experiments; darkening of the upper or lower part of the shoot was employed in the first and second; a combination of defoliation and darkening served in the third and fourth.

RESULTS

Upper or Lower Parts of the Treated Plant in the Dark. Some actual turgor values obtained in two of the experiments are presented in Table I to indicate general magnitude and variation. Phloem pressure was lowered in the darkened areas. Turgor differences between the source region (P_2) and other stem regions (P_1 or P_3) were greater in the case of the treated plants than in controls. A mean pressure difference of 3.8 atm was found between the treated leaf node and the darkened upper shoot, compared to −0.1 atm in the controls. Darkening the lower shoot reduced the pressure in that region, accounting for a mean pressure difference of 5.1 atm (Table II). Differences in pressure between the upper and lower parts of each plant were greater in treated plants compared to controls. This indicates that darkening had definite effects in increasing pressure differences between source and darkened regions. Accumulation of labeled compounds was higher in the darkened parts than in the controls. The mean percentage of radioactive distribution was 17.93% in the darkened upper shoot, compared to 7.38% in the controls. Where the lower shoot was darkened, the corresponding values were 21.64% and 11.87% (Table III). Differences in percentage of radioactivity between the upper and lower

Table I. *Representative phloem turgor values obtained with the phloem needle in two shoot darkening experiments. Measurements were made in three stem locations: P_1, upper shoot; P_2, region of $^{14}CO_2$-treated leaf; P_3, lower shoot.*

	Pressure in atmospheres						
Replication	P_1	P_2	P_3	Replication	P_1	P_2	P_3
	Controls				Controls		
1	2.2	2.1	2.3	1	2.3	2.2	2.0
	2.3	2.3	2.7		2.2	2.2	3.0
2	3.7	2.0	1.2	2	3.5	3.0	1.5
	4.3	2.6	1.7		4.5	1.6	1.4
3	0.5	7.9	5.8	3	0.6	7.8	6.9
	0.7	7.9	7.9		0.6	8.0	6.8
4	0.7	1.5	1.3	4	0.6	2.3	1.2
	0.6	2.5	1.5		0.7	1.7	1.6
	Upper shoot in dark				Lower shoot in dark		
1	0.3	4.2	1.0	1	3.1	10.4	2.0
	0.3	4.8	0.6		2.8	8.2	1.4
2	0.5	4.1	0.5	2	3.0	10.2	1.3
	0.3	4.4	6.4		3.3	9.9	1.0
3	0.4	2.5	0.8	3	4.2	8.0	0.9
	0.4	2.6	0.5		4.4	8.0	0.6
4	1.2	6.7	3.4	4	0.9	8.5	0.6
	1.6	5.5	4.3		1.8	1.9	0.4
5	2.6	7.0	3.2	5	1.0	3.0	0.4
	2.4	6.5	3.7		1.5	2.3	0.4
6	1.9	5.5	3.1	6	0.7	3.2	0.4
	1.6	4.9	2.2		0.9	2.8	0.4

parts of the plants were significantly greater in treated plants compared to controls. Autoradiographs of several cross-sections of the stem and samples of leaves and roots showed more radioactive assimilate movement to the darkened regions.

Combination of Darkening and Defoliation. In order to minimize the source and sink effects of the other leaves in the light and assure that only the treated leaf functioned as a single source of photosynthate, all of the leaves below or above the treated leaf were removed 24 hr before application of $^{14}CO_2$. When the upper parts of the treated plants were darkened, the lower parts of the control and treated plants were defoliated; and when the lower parts of the treated plants were darkened, the upper parts of the control and treated plants were defoliated.

Darkening the upper part of the plant induced a stronger sink than developed in the defoliated lower shoot and roots. A pressure difference of 5.3 atm between the treated leaf and darkened upper shoot was recorded, compared to 2.4 atm in the controls (Table II). When pressure differences $P_2 - P_1$ and $P_2 - P_3$ are compared, it is seen that mean differences between $(P_2 - P_1)$ and $(P_2 - P_3)$ are greater in the treated plants than in controls. A higher percentage of radioactive tracer moved to the darkened region, where pressure was lower, compared to controls. The mean percentage of radioactivity was 22.32% in the upper part of the shoot in treated plants as compared to 7.38% in controls (Table III). Results of one-way analysis of variance showed significant effects of darkening on induction of the sink and distribution of radioactive assimilates in this region. Figure 1 shows autoradiographs of control and treated plants. More labeled material moved into the upper part of the treated plant compared to the control. Autoradiographs representing results of other shoot manipulation experiments were prepared in similar manner and appear elsewhere (19).

In experiments where upper parts of the shoots were defoliated, darkening of the lower parts of the treated plants produced no significant differences in pressure between controls and treatments (Table II). This is explained by the fact that the major sinks such as roots and developing axillary shoots were located in the lower part of the plant. Radioactive assimilate moved toward the sink regions in the lower part of the plant, and one-way analysis of variance showed insignificant differences in percentage of radioactivity in both controls and treatments (Table III). Autoradiographs of the samples of various plant parts showed accumulation of tracer materials in the sink regions, mostly in the lower parts of both control and treated plants, with slightly more radioactivity in the treated plant.

Table II. *Means of phloem turgor pressure differences in the upper and lower parts of the plants in darkening and defoliation experiments*

	Manipulation	Pressure in atmospheres: Pressure differences between treated leaf P_2 and upper part P_1	Pressure differences between treated leaf P_2 and lower part P_3	Difference between columns 1 and 2
Control		-0.1	0.3	-0.4 ± 0.7
Treated	Upper part in dark	3.8	3.0	0.8 ± 0.3
Control		1.7	0.4	-1.3 ± 1.9
Treated	Lower part in dark	3.6	5.1	1.5 ± 0.4
Control	Lower part defoliated	2.4	2.8	-0.4 ± 0.6
Treated	Lower part defoliated; upper part in dark	5.4	4.1	1.3 ± 0.2
Control	Upper part defoliated	2.6	3.6	1.0 ± 0.6
Treated	Upper part defoliated; lower part in dark	2.9	4.1	1.1 ± 0.3

Table III. *Means of radioactive distribution in darkening and defoliation experiments. Data are expressed as percentages of total radioactive distribution and are evaluated with the one-way analysis of variance method*

	Manipulation	% of total radioactive distribution: Above the treated leaf	Below the treated leaf	Diff.	F. value
Control		7.38	11.87	-4.49	12.97***
Treated	Upper part in dark	17.93	6.44	11.49	
Control		7.38	11.87	4.49	6.21*
Treated	Lower part in dark	10.27	21.64	11.36	
Control	Lower part defoliated	7.93	30.57	-22.64	7.70*
Treated	Lower part defoliated; upper part in dark	22.32	6.30	16.01	
Control	Upper part defoliated	9.59	23.31	13.62	1.38
Treated	Upper part defoliated; lower part in dark	3.77	27.71	23.93	

*Significant at 0.05
***Significant at 0.01

DISCUSSION

Of the three so-called water quantities, water potential (ψ), pressure potential (ψ_p), and osmotic potential (ψ_π), ψ_p has been the most difficult to measure. Osmotic gradients in sieve tubes can be determined by measuring ψ_π of phloem exudates. The ψ_π value determines the maximum turgor that could develop in the sieve tube when ψ of the surrounding tissues is zero. Since ψ is not usually zero, but something less, the turgor value is unknown. Measuring ψ_π and ψ of leaf, stem, or root, as appropriate, would permit the indirect determination of sieve tube turgor from the relation $\psi_p = \psi - \psi_\pi$. However, the values might be somewhat less acceptable than those from direct measurements. It is of interest that ψ_π values have been found to be less (more negative) in source areas than in sinks (30), and this corresponds generally with measurements of ψ_p in *Ecballium*, values being higher in sources than in sinks.

The results with *Ecballium* confirm the usefulness of the phloem needle method for turgor determination as introduced by Hammel (13). To date, it is the only method available. Hammel measured the pressure in the secondary phloem of red oak trees at heights of 1.5 and 6.3 m. The pressures were higher in the upper parts of the trees which had more leaves and were considered the source region, compared to pressures at 1.5 m. The values ranged from 19.5 atm in the upper level to 7.6 atm in the lower level of the plant for a variety of weather conditions.

When the phloem needle was pressed into the *Ecballium* stem, vascular bundles infrequently were missed, the needle tip lodging in parenchyma and no measurement could be made. The parenchymatous cells probably had a substantial turgor pressure, but the volume of cell sap released from them by needle penetration was insufficient to cause compression of the air column in the capillary. In addition, some of the sap may have moved into intercellular spaces. It seems that this device is rather uniquely suited to determining turgor values of sieve elements, and is not useful for other cell types. The success of the needle measurement is clear evidence of axial sap mobility within sieve tubes. One may also conclude that the sieve plates do not obstruct flow to any great extent. Success, also, is due to the rigidity and tightness of the phloem tissue, with intercellular spaces essentially lacking. Release of sap into the spaces would make the method useless.

The values obtained probably represent average pressures existing in several ruptured sieve tubes, since the needle diameter, about 0.3 mm, is larger than the diameter of a single sieve tube. It has to be assumed that the pressure values are slightly less than those that existed in the intact sieve tubes because of the loss of exudate into the capillary. It has not been possible to assess this error. In any event, the error would tend to cancel out somewhat where pressure differences were calculated. Error in measurement due to leakage around the needle probably was insignificant, since length of the compressed air column remained constant over the reading period of up to a minute.

The possibility exists that after making one measurement, a second needle insertion 15 cm above or below the first would tap the same bundle. If so, one wonders if the exudate loss from the first puncture would reduce the turgor in the region of the second measurement. It seems unlikely that the same track would be tapped in successive measurements, first of all because of the presence of 12 to 15 bundles in the stem cross-section, and secondly, because care was taken to move around the stem to avoid hitting the same bundle.

One would expect some variation in pressure even at one stem level, where several readings are taken at points around the stem. This would be due to the fact that different strands of phloem may be connected to different leaves, which might func-

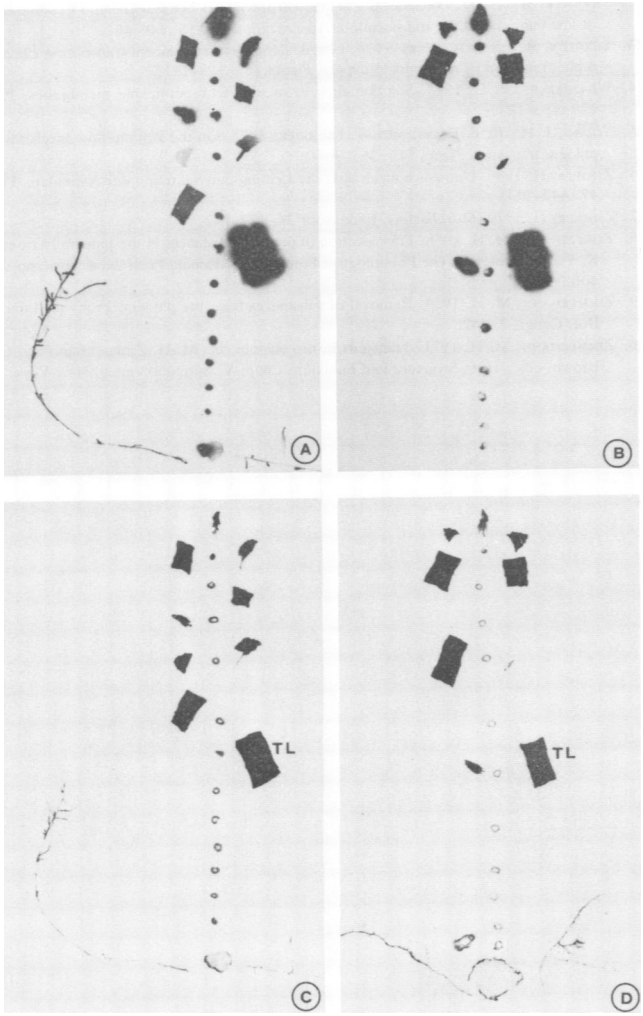

FIG. 1. Translocation of ^{14}C-assimilates in *Ecballium* plants. $^{14}CO_2$ was applied to a single leaf (TL). Lower parts of the control and treated plants were defoliated; the upper parts of the treated plant (D) were darkened. The autoradiograph shows that most of the labeled assimilate moved to the upper parts of the treated plant (D). Autoradiographs (A and B) of mounted sections of control (C) and treated (D) plants are shown, respectively.

tion either as source or sink depending on their developmental stage. The pattern of leaf development of *Ecballium* plants used in the present work was such that the shoot possessed mature and developing leaves both in the upper and lower parts of the plant.

Thrower (22) studied changes in the ^{14}C-assimilate export by developing leaves of soybean. No export of the label occurred when the leaf area was less than 30% of adult size; thereafter export increased, an overlap being found between 30 and 50% of the adult size, when the leaf is simultaneously importing and exporting. Turgeon and Webb (23) showed that the capacity of a growing leaf blade of *Cucurbita pepo* to import ^{14}C-labeled photoassimilate is lost first in the tip, progressing toward the base. At a particular developmental stage, then, export proceeds from the more mature leaf tip while import continues into the relatively immature leaf base. Import into the tip stops when the blade is 10% expanded and the laminar base stops importing when the blade is 45% expanded. The authors showed that export capacity also develops basipetally and immediately follows the loss of import capacity.

In the present studies, it was clearly shown that darkening and defoliation of different parts of the plant intensified sinks for assimilate translocation. Corresponding to the lower turgor levels induced, and the higher pressures in sources than in sinks, is the demonstrated increase of translocation rate. Others have reported results that demonstrate the importance of sinks for transport. Habeshaw (12) showed that the size and activity of sinks for products of photosynthesis have a large control over carbohydrate levels in the source leaves of the sugar beet plant, and hence an effect on the rate of translocation. Quinlan and Weaver (18) reported that application of 4.4 mM benzyladenine, a cytokinin, to the leaves of *Vitis*, caused a marked increase in ^{14}C import by the leaf due to stimulation of sink activity.

Darkening of the upper or lower shoot regions of the *Ecballium* plant 24 hr before $^{14}CO_2$ application probably would result in utilization of any stored carbohydrate, and would make them dependent on source leaves receiving light. Darkening by preventing photosynthesis would change the function of leaves 30 to 50% mature from simultaneous exporting and importing to only importing. This could be interpreted as relatively increasing sink activity. Geiger and Batey (11) have demonstrated that polysaccharide reserves in darkened leaves of *Beta* begin to contribute to the translocation stream after 2 to 3 hr of darkness.

There is scant evidence in the literature that mature leaves can change from exporting to importing as a result of darkening. In studies of ^{14}C translocation in detached leaf segments of *Zea mays*, Heyser *et al.* (15) found that darkening of a region caused it to behave as a strong sink. The normal basipetal movement of assimilate could be reversed by darkening the apical end of the segment. Similarly, Hartt and Kortschak (14), using detached leaves of sugarcane, found that the direction of assimilate transport could be reversed by darkening.

Darkening or defoliation of the upper or lower parts of the *Ecballium* plant probably would raise the water potential of the xylem and secondarily of the phloem. This effect is considered to be negligible compared to the inhibitory effect of darkening on photosynthesis and the resulting decrease in phloem turgor pressure in the darkened areas.

The volume flow hypothesis (9, 25) referred to earlier considers flow to proceed as a function of the water potential difference across the sieve tube plasmalemma, not necessarily involving a pressure gradient. The fact that pressure differences do occur and can be measured indicates that there is resistance to flow in the conduits, probably due to both sieve tube lumina and sieve plates. Calculations based on flow in tubes equivalent in size to sieve tubes suggest that pressure differences are not negligible (24).

The correlations observed between phloem pressures and assimilate distribution lend support to the pressure flow mechanism of sieve tube translocation.

LITERATURE CITED

1. BAUER, L. 1953. Zur Frage der Stoffbewegungen in der Pflanze mit besonderer Berucksichtigung der Wanderung von Fluorochromen. Planta 42: 367-451.
2. CRAFTS, A. S. 1961. Translocation in Plants. Holt, Rinehart and Winston, New York.
3. CRAFTS, A. S. 1967. Absorption and translocation of labeled tracers. Ann. N. Y. Acad. Sci. 144: 357-361.
4. CRAFTS, A. S. AND C. E. CRISP. 1971. Phloem Transport in Plants. W. H. Freeman & Co., San Francisco.
5. ESAU, K. 1967. Anatomy of plant virus infections. Annu. Rev. Phytopathol. 5: 45-76.
6. ESAU, K. J. CRONSHAW, AND L. L. HOEFERT. 1967. Relation of beet yellows virus to the phloem and to movement in the sieve tube. J. Cell Biol. 32: 71-87.
7. ESCHRICH, W. 1967. Bidirektionelle Translokation in Siebröhren. Planta 73: 37-49.
8. ESCHRICH, W., H. B. CURRIER, S. YAMAGUCHI, AND R. B. MCNAIRN. 1965. Der Einfluss verstärkter Callosebildung auf den Stofftransport in Siebröhren. Planta 65: 49-64.
9. ESCHRICH, W., R. F. EVERT, AND J. H. YOUNG. 1972. Solution flow in tubular semipermeable membranes. Planta 107: 274-300.
10. FISHER, R. A. 1947. The Design of Experiments, Ed. 4. Oliver and Boyd, Edinburgh.
11. GEIGER, D. R. AND J. W. BATEY. 1967. Translocation of ^{14}C-sucrose in sugarbeet during darkness. Plant Physiol. 42: 1743-1749.
12. HABESHAW, D. 1973. Translocation and the control of photosynthesis in sugar beet. Planta 110: 213-226.
13. HAMMEL, H. T. 1968. Measurement of turgor pressure and its gradient in the phloem of oak. Plant Physiol. 43: 1042-1048.

14. HARTT, C. E. AND H. P. KORTSCHAK. 1964. Sugar gradients and translocation of sucrose in detached blades of sugarcane. Plant Physiol. 39: 460–474.
15. HEYSER. W., O. LEONARD, R. HEYSER, E. FRITZ, AND W. ESCHRICH. 1975. The influence of light, darkness, and lack of CO_2 on phloem translocation in detached maize leaves. Planta 122: 143–154.
16. MOORE, T. C. 1968. Translocation of the growth retardant *N, N*-dimethylaminosuccinamic acid-^{14}C. Bot. Gaz. 129: 280–285.
17. MÜNCH, E. 1930. Die Stoffbewegungen in der Pflanze. Gustav Fischer, Jena.
18. QUINLAN, J. D. AND R. J. WEAVER. 1969. Influence of benzyladenine, leaf darkening, and ringing on movement of ^{14}C-labeled assimilates into expanded leaves of *Vitis vinifera* L. Plant Physiol. 44: 1247–1252.
19. SHEIKHOLESLAM, S. N. 1975. Turgor Pressure Gradients, Phloem Translocation, and Effects of Water Stress on Structure and Function of Sieve Tubes. Ph.D. dissertation. Univ. of California, Davis.
20. TAMMES, P. M. L. 1938. Micro- and macro-nutrients in sieve-tube sap of palms. Acta Bot. Néerl. 7: 233–234.
21. TAMMES, P. M. L. AND J. VAN DIE. 1966. Studies on phloem exudation from *Yucca flaccida* Haw. IV. Translocation of macro- and micro-nutrients by the phloem sap stream. Koninkl. Ned. Akad. Wetenschap. Proc. (C) 69: 655–659.
22. THROWER, S. L. 1962. Translocation of labelled assimilates in the soybean. IV. Some effects of low temperature on translocation. Aust. J. Biol. Sci. 18: 449–461.
23. TURGEON, R. AND J. A. WEBB. 1973. Leaf development and phloem transport in *Cucurbita pepo:* transition from import to export. Planta 113: 179–191.
24. WEATHERLEY, P. E. 1973. Solution flow in tubular semi-permeable membranes. Planta 110: 183–187.
25. YOUNG, J. H., R. F. EVERT, AND W. ESCHRICH. 1973. On the volume-flow mechanism of phloem transport. Planta 113: 355–366.
26. ZIEGLER, H. 1956. Untersuchungen über die Leitung und Sekretion der Assimilate. Planta 47: 447–500.
27. ZIEGLER, H. 1970. Morphactins. Endeavour 24: 112–117.
28. ZIMMERMANN, M. H. 1958. Translocation of organic substances in the phloem of trees. *In:* K. V. Thimann, ed., The Physiology of Forest Trees. Ronald Press, New York. pp. 381–400.
29. ZIMMERMANN, M. H. 1959. Removal of substances from the phloem. Proc. 9th Internatl. Bot. Congr. 2: 442.
30. ZIMMERMANN, M. H. 1971. Transport in the phloem. *In:* M. H. Zimmermann and C. L. Brown, eds., Trees Structure and Function, Chap. V. Springer-Verlag, New York.