TRANSLOCATION OF ORGANIC SUBSTANCES IN TREES. II. ON THE TRANSLOCATION MECHANISM IN THE PHLOEM OF WHITE ASH (FRAXINUS AMERICANA L.)[1]

MARTIN H. ZIMMERMANN

CABOT FOUNDATION, HARVARD UNIVERSITY, PETERSHAM, MASSACHUSETTS

The mechanism of phloem translocation is a major problem. A simple and plausible theory, the mass flow theory, has been proposed by Münch in 1930 (17). The driving force presumably is a difference in turgor pressures. In the leaves, where organic material is synthesized, the osmotic pressure is high. In stem and roots, where assimilates are removed for growth and storage, the osmotic pressure is low. According to Münch, the resulting turgor pressure difference automatically forces vascuolar sap from places of production to places of consumption. The alternative theories are less clearly outlined. They differ from the mass flow theory in supposing that the organic molecules are metabolically or physically translocated, but do not move as a solution in bulk.

Much evidence for and against mass flow has been presented since 1930, but no final decision can yet be made, because most of the disagreements rest upon interpretation of the data. However, if mass flow does occur, it seems to be restricted to the sieve elements of the phloem. Translocation from the parenchyma cells of the leaves into the sieve elements may occur against a concentration gradient (19) and chemical transformations are considerably involved (10, 25, 27). Removal of sugars from the sieve tubes also seems to be a metabolic process (27, 29). Chemical constituents within the sieve tube system, however, were found to be qualitatively the same throughout the plant (10, 16, 26, 27). These chemical findings are not surprising because anatomists observed many years ago that the metabolic activity of sieve elements must be reduced: their protoplast lacks a nucleus when the cell completes its development and becomes functional (5).

There are three basic requirements for a passive movement of solutes along a turgor pressure gradient:

1st. The cytoplasm lining the longitudinal walls of the sieve tubes must be semipermeable.

2nd. The sieve plates, however, must be permeable to the translocated solution.

3rd. The turgor pressure gradient must be positive in the direction of flow.

Some advocates of Münch's theory believe today that a passive mass flow through the sieve elements is indirectly maintained by the metabolic activity of the sieve tube cytoplasm and the surrounding tissue, particularly the companion cells. In the leaves, assimilates are secreted into the vacuole of the sieve elements, in stem and roots they are metabolically removed. Thus a concentration gradient is established and maintained.

[1] Received March 14, 1957.

Although the turgor gradient has to be positive in the direction of flow, according to the mass flow theory, the turgor itself does not necessarily have to be positive. Mass flow may be "suction"-flow as well as "pressure"-flow. This has extensively been investigated by Frey-Wyssling (6). Metabolic removal of organic material from the sieve elements (e.g., through starch formation) must be followed by a loss of a corresponding amount of water. This results in a turgor drop and, if requirements one and two are fulfilled, in a flow of vacuolar sap toward the point of removal of organic material.

In the experiments here reported an attempt has been made to investigate the three conditions necessary for mass flow to occur, using white ash as experimental material. There are several advantages of studying phloem translocation by means of chromatographic analysis of sieve tube exudate of trees. Since it is quite likely that various chemical reactions account for entry of solutes into and exit from sieve elements, and since translocation from the parenchyma cells in the leaves into the sieve tubes occurs against a concentration gradient, osmotic pressure determinations of whole organs or even vascular bundles are no indication of the osmotic pressure within the sieve tubes. Evidence indicating that sieve tube exudate of trees represents translocated material has been previously discussed (28). Crafts and Lorenz (3) stated that "phloem exudate from cucurbits can no longer be considered as a true sample of the assimilate stream." This statement is based upon the observation that nitrogen content of phloem exudate from cucurbits is much higher than the nitrogen content of their fruits. This does not hold, however, for trees. Nitrogen content in exudate of trees is very low indeed (16, 27, 29). Furthermore, exudation from one tapping cut lasts a considerable length of time in many trees, in white ash for instance, for half an hour or longer. The material, therefore, originates from the sieve tubes far above the cut. This is also indicated by the observation of Hartig (7, 8) and Münch (17) that the sieve tube turgor is reduced up to several meters above the tapping cut.

The situation in a large forest tree is a much clearer one than that in a small herbaceous plant. In order to investigate gradients, we can take samples of sieve tube exudate from places on the trunk which are far apart but nevertheless physiologically comparable, and clearly separated from the place of assimilate production. Moreover, we do not have to cut the entire conducting system like in cucurbits, but disturb only a very small fraction of the whole phloem with each cut.

The total molar concentration gradient is undoubtedly a very close measure of the turgor gradient, it is therefore relatively easy to investigate the third requirement. It is much more difficult, however, to investigate the properties of the sieve tube cytoplasm. One approach is the plasmolysis experiment. Mature sieve tubes are difficult to plasmolyze and great skill is needed for this operation (4, 20), but this difficulty may be due only to their longitudinal permeability. Thus application of a solution of high osmotic value may cause a flow of vacuolar sap through the sieve tubes toward the point of application, rather than plasmolysis of individual sieve elements. The interpretation of plasmolysis experiments is still being debated (1, 4, 21). In the experiments here reported an attempt has been made to approach the problem of semipermeability in a different way.

Experimental

All experiments were carried out on trees in the Prospect Hill tracts I, II and IX of the Harvard Forest. Sieve tube evudate was obtained from white ash by cutting into the bark as previously described (28). The samples were immediately taken up with numbered pipettes, calibrated at 1 (for mannitol analysis), 4 (sugars) or 5 (sugars, amino-acids) lambdas and transferred to the starting point of paper chromatograms. As soon as these were dry they were wrapped in polyethylene foil and placed in a freezer at $-20°$ C. Each package contained the analytical work for one day, i.e., 56 sugar analyses including 16 reference values of known amounts.

The identification of the oligosaccharides (sucrose, raffinose and stachyose) in the sieve tube exudate of white ash has been previously described (28). Whatman No. 1 paper was used in a descending procedure throughout. The partitioning solvent was *n*-butanol : acetic-acid : water = 3 : 3 : 2 v/v, which yields even separation of sucrose, raffinose and stachyose within 24 to 30 hours. Each chromatogram contained five exudate samples, three for localization of the sugar positions and two for analysis. After separation the paper was cut into five strips and the three reference strips developed with a resorcinol reagent (28) for localization of the sugar positions. The elution process is shown in figure 1. Each sugar is cut out and eluted from the paper into test tubes by a chromatographic process using distilled water. The racks were welded from 1/16″ polyethylene sheet. Each rack holds 8 test tubes calibrated at 5 ml and numbered. Since the elution process must take place in a moist atmosphere, each rack was covered with a glass jar. To achieve the same blank value for every sample the short paper pieces (usually raffinose, sometimes also stachyose) were brought to the standard length by adding a piece of blank paper previously treated, like the chromatograms, with the partitioning solvent. During elution the oligosaccharides were enzymatically hydrolyzed with 10 lambdas of an invertase solution (Nutritional Biochemical Co.) placed on the tip of each paper before elution. This

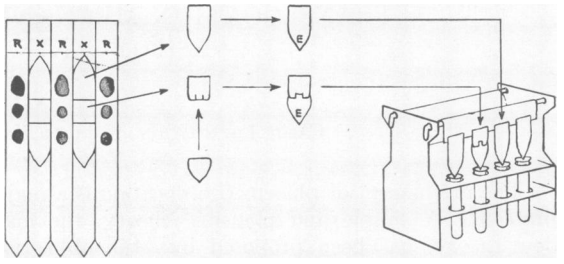


Fig. 1. Elution and hydrolysis of sugars. The chromatogram is cut into five strips, of which three reference strips (R) are developed for localization of sugar positions. Sugars to be analyzed (on strips X) are cut out, the short pieces containing raffinose brought to standard length by adding a piece of blank paper. Ten lambdas of invertase is placed on tip of each paper (E). Papers containing sugars are attached to filter paper whose opposite end dips into the water in the trough of elution rack. To keep the atmosphere moist during elution, the racks are covered with glass jars. The sugars are eluted for 5 hours in the presence of toluene (to prevent infections). At the same time they are hydrolyzed (fructose unit split off) by the enzyme.

enzyme splits off the fructose unit of each sugar. Special attention was necessary to prevent infection during the elution and hydrolysis process. It is practically impossible to keep the set-up completely sterile. Antisiphon rods, anchor rods and filter paper were heated and the polyethylene racks exposed to strong ultraviolet light before use. Toluene was placed in the trough of the elution rack and a few drops introduced into each test tube. Elution and hydrolysis were complete after 5 hours. In order to avoid losses by infection, no longer time should be used. After elution the volume in each test tube was brought to 5 ml with distilled water and the sugar determination carried out with Somogyi's method (22), as modified by Nelson (18). The reaction of sucrose and raffinose was the same for same molar amounts, that is, the reaction intensity of glucose and melibiose were the same under our conditions. The calibration curve obtained from sucrose and raffinose reference values could also be used for stachyose determinations, because the fructose molarity of inverted exudate samples was found to be the same as the total molarity of the three sugars determined with the described procedure.

The quantitative determination of mannitol was carried out by transmission densitometry after the chromatograms had been developed with an alkaline silver nitrate reagent (24). Because transmission densitometry is much less accurate than chemical methods, a large number of samples have been analyzed for each needed value.

Semipermeability of the Sieve Tube Cytoplasm: The physiological properties of the sieve tubes required by the mass flow theory of Münch (17) are rather peculiar. The whole sieve tube system must behave somewhat like a single giant cell. The con-

centration of its contents has been shown to be 10 to 30 grams per 100 ml of sap (7, 8, 13, 17, 27). About 90 % of the solutes are sugars, either sucrose alone (13, 26, 27, 28), or accompanied by higher oligosaccharides (28). Sieve tube exudate of ash contains also a large amount of mannitol (up to 0.2 molar in white ash). The high concentration of the sieve tube or sieve cell sap produces a corresponding turgor within the sieve tube system which causes an elastic expansion of the cells. When the system is severed by a tapping cut, some sap is forced out within a few seconds by the elasticity of the cell walls. Many trees, e.g., conifers, cannot be tapped, however. This has been claimed to be evidence against mass flow. However, current investigations by Mittler (14, 15, 16) with cut-off stylets of aphids seem to promise that exudate can be obtained from any plant with functional sieve elements. In most trees tapping causes an explosion-like exudation due to elastic contraction of the sieve tubes. The flow then stops, probably because of a plugging of the sieve plates at the moment of the pressure release (2, 12). In other trees, such as white ash, flow continues slowly for about half an hour or longer.

As soon as the pressure is released by tapping, water enters the system from the surrounding tissue thus diluting the exudate. This dilution, which begins at the moment the cut is made, can be measured. Ash trees about 5 cm in diameter were tapped by a 2-cm long cut. Samples were taken with numbered pipettes graduated at 5 lambdas. After the first sample had been taken the excess sap, exuded because of the immediate elastic contraction of the sieve tubes, was usually blotted from the cut. Subsequent samples were taken as soon as possible. During the month of August, 6 to 12 samples could be obtained within about half an hour. (From about mid-September on the sap flow greatly increases, its concentration decreases and the dilution effect decreases. This indicates a greater longitudinal permeability of the sieve tubes. Seasonal changes have been discussed elsewhere (29)). It was necessary to work on calm days to avoid an increase in concentration caused by drying of the sap on the cut surface. Moreover, the cut was carefully shielded with Scotch tape and only a small opening left for the pipettes. The sugar concentration of the exudate decreased continuously. Figure 2 shows an experiment carried out on August 20, 1956. In the last sample, taken 25 minutes after the cut was made, the concentration had dropped to about 70 % of that in the first one. The same dilution effect was observed by Frey-Wyssling in the latex of Hevea (6). The results of Crafts (3) and Tingley (23) show a similar trend in the phloem of cucurbits, but since the exudation in cucurbits is small, and less subtile methods were available in 1944, the dilution was found through a series of cuts.

Further evidence for the semipermeability of the cytoplasm lining the side walls of the sieve tubes is the following observation. The sieve tube system does not leak; it retains the sugars even for a day or

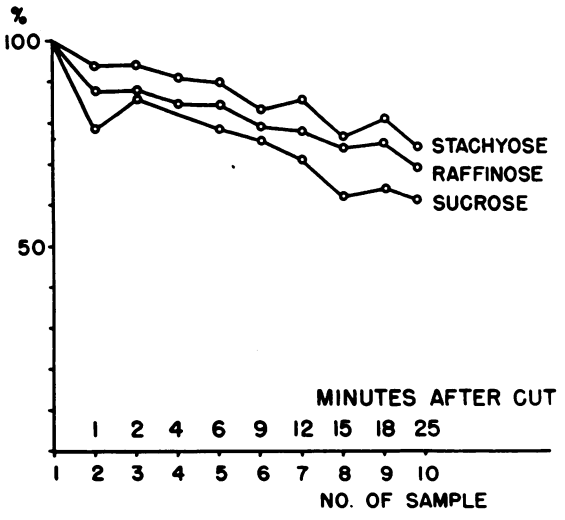


FIG. 2. Osmotic dilution effect in the sieve tube system of white ash (Aug. 20, 1956). Subsequent samples taken from one tapping cut show a continuous decrease in concentration. The cut yielded sap for about half an hour. The sugar concentrations are shown in percent of the concentrations in the first sample which are: stachyose 0.242 M, raffinose 0.077 M, sucrose 0.068 M.

two after all the leaves have dropped in the fall (cf fig 4). During this time the sugar concentration decreases continuously by the activity of an enzymatic removal system (29).

The gradients also suggest that the side wall cytoplasm of the sieve tubes is semipermeable. If the sieve tubes were leaking the gradients had to correspond with the molecular sizes. In other words, the smallest molecule, mannitol, had to have the steepest gradient, the largest molecule, stachyose, the gentlest. However, the gradients have never been found to be correlated with the molecular size. The molecules must be metabolically removed from the sieve tubes.

PERMEABILITY OF THE SIEVE TUBES IN THE LONGITUDINAL DIRECTION: The flow of exudate from a tapping cut indicates that the sieve plates are permeable for the solution. After the first explosion-like exudation which is due to the release of the elastic tension of the sieve tubes (17), the flow continues for about half an hour. The dilution effect indicates that this second stage of exudation is maintained by osmosis. The question is whether the same kind of solute movement occurs under natural conditions. If the tapping process were a severe disturbance and the solute flow an artifact, the sieve tubes, and especially the sieve plates immediately above the cut would be seriously damaged and could no longer function. (The turgor is released up to several meters above the cut (17).) We found, however, that any time after tapping (from half an hour to several weeks later), the sieve tubes above the cut can be tapped again. They are not damaged by tapping. Therefore, it does not seem likely that the permeability of the sieve plates is an artifact.

CONCENTRATION GRADIENTS IN THE SIEVE TUBE SYSTEM: No matter where we tap the tree, 15 meters above the ground near the leaves, or at the base of the trunk, the content of the exudate is qualitavely the same. The concentration varies from tree to tree and fluctuates somewhat diurnally (13, 27, 29) and seasonally (29). Concentrations of the substances found in white ash were usually within the following values:

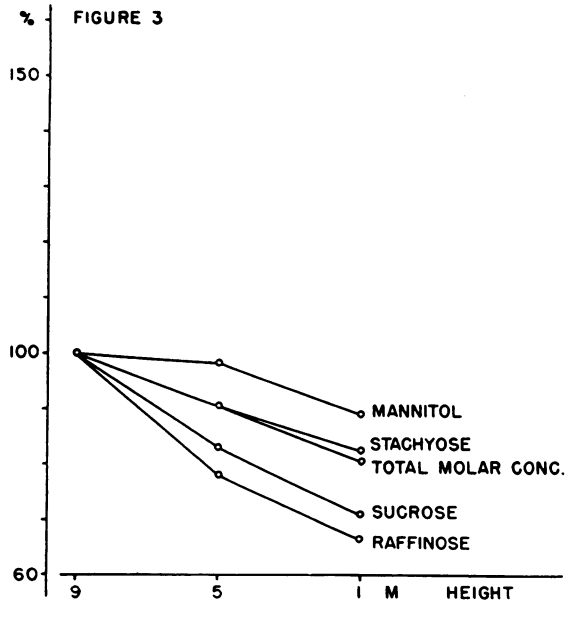
Sucrose, 0.05–0.15 M
Raffinose, 0.05–0.1 M
Stachyose, 0.15–0.3 M
Verbascose, trace
(No reducing sugars, no sugar phosphates)
Mannitol, 0.05–0.2 M

Amino-acids and amides usually less than 0.001 M total, mainly glutamine and glutamic acid.

Traces of substances absorbing or fluorescent in ultraviolet light.

Samples were taken from a tree 20 to 30 cm in diameter at 3.5-hour intervals during 24 hours at 1, 5 and 9 meters height. This was repeated with many trees during the summer months of 1955 and 1956. Although gradients showed slight diurnal variations as reported elsewhere (29), they were always positive in the downward direction of the trunk. Only one substance, fluorescent in 365 mμ when exposed to short ultraviolet light, increased in concentration in the downward direction. The concentration of this substance was measured on the chromatogram by transmission densitometry. The substance is also present in winter when there is no phloem exudation at all. One drop of water applied at this time on a fresh cut and immediately picked up again contained about as much of the fluorescent substance as a sample of sieve tube exudate obtained in summer. This suggests that it does not originate in the sieve tubes but is eluted from the bark tissue during the tapping process.

The substances present in sufficient concentrations to account for an osmotic pressure difference are sucrose, raffinose, stachyose and mannitol. Substances other than sugars and mannitol have been found to represent only about 10 % of the total dry weight. Since the concentration differences over a length of 8 meters are around 20 % the described gradients cannot be affected more than 2 % by other substances. Concentration gradients are shown in figure 3. Although all four substances decrease in concentration on their way down the trunk, they do not decrease at the same rate in every individual tree. In other trees, for instance, stachyose showed the greatest decrease, raffinose decreased less, sucrose least, and so forth. This decrease is ascribed to the removal mechanisms which have been discussed elsewhere (29).



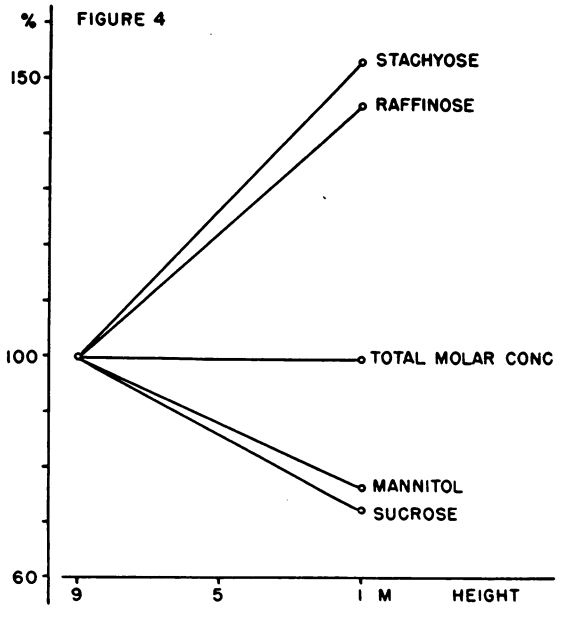


FIG. 3. Typical gradients in sieve tube exudate of white ash (July 30/31, 1956). Concentrations are shown in percent of the 9-meter values, which are: sucrose 0.082 M, raffinose 0.073 M, stachyose 0.202 M, mannitol 0.178 M. Values at each height are average values of 24 samples taken at 3.5-hour intervals during 24 hours. Concentration gradients were always positive in the downward direction of the trunk throughout the summer.

FIG. 4. Gradients of the four substances that can account for an osmotic pressure difference (Oct. 8, 1956, after all leaves have dropped). Concentrations are shown in percent of the 9-meter values, which are: sucrose 0.138 M, raffinose 0.034 M, stachyose 0.099 M, mannitol 0.136 M. Values at each height are average values of 32 samples from 16 cuts around the trunk. Some gradients are negative in the downward direction and the total molar gradient has almost disappeared. The gradient inversion begins when the leaves turn yellow. This figure shows a late stage.

Important for us at this point is the fact that the four substances do decrease at different rates, whatever is the cause. What should happen, according to the mass flow theory, at the time the leaves cease to supply material to the sieve tubes? The flow should continue as long as there is a turgor difference at the different levels (high up in the tree near the leaves, and at the base of the trunk). There will be a turgor difference as long as there is a difference in the total molar concentration in the sieve tubes. If there is only one osmotically active substance (e.g., sucrose), the flow will slow down and finally stop completely when the concentration reaches the same value everywhere. If there are several substances and their concentration gradients are different, the substances with the smallest gradients—still according to the mass flow theory—have to be moved against their gradients until the total molar gradient disappears. This, of course, is only strictly true if the total molar concentration gradient is identical with the turgor gradient. However, at this point, we are mainly interested in the change that takes place when the leaves cease to supply assimilates to the phloem.

Experimental results indicate that this actually happens in the fall. The sieve tubes can be tapped until one or two days after all the leaves have dropped. Figure 4 shows an experiment where 32 samples (from 16 cuts around the trunk) have been taken at 1 and 9 meters respectively from a tree whose leaves had all dropped. Stachyose and raffinose show a large negative, sucrose and mannitol a postive gradient. The gradient of the total molar concentration is practically zero. This gradient inversion, a typical autumn effect, starts to appear when the leaves turn yellow and begin to drop.

The results here presented are in agreement with the mass flow theory of Münch (17), according to which translocation takes place through the vacuole of the sieve tubes, a difference in the total turgor pressure being the driving force of translocation. Indeed, it would be very difficult to interpret them in terms of a metabolic transport. We do not know, however, to what extent these conclusions, drawn from experimental results with white ash are applicable to other plants. Huber found very large sieve pores (up to 15μ in diameter) in *Fraxinus excelsior* and these have no callose cylinder (9, 10, 11). However, many other plants have rather small pores usually filled with cytoplasm. The fact that investigators are not in agreement on the translocation mechanism may not be due only to individual interpretation of results, but also to the variety of plants used for experimental work, and it would not be surprising if there were more than one single mechanism that can account for the translocation through the phloem.

Summary

Sieve tube exudate of white ash (*Fraxinus americana* L.) has been analyzed. The same substances are found in all parts of the tree. Their concentrations vary somewhat from tree to tree: Sucrose 0.05 to 0.15 M; raffinose 0.05 to 0.1 M; stachyose 0.15 to 0.3 M; a trace verbascose; mannitol 0.05 to 0.2 M; amino-acids and amides usually less than 0.001 M, mainly glutamine and glutamic acid; traces of substances that are absorbing or fluorescent in the ultraviolet light. No reducing sugars and no sugar phosphates have been found.

There are three basic requirements for Münch's mass flow mechanism through the sieve tubes: 1) The cytoplasm lining the longitudinal walls of the sieve tubes must be semipermeable. 2) The sieve plates must be permeable for the transported solution. 3) The turgor gradient must be positive in the direction of flow. Experimental results with white ash are all in agreement with these requirements:

1. Three observations indicate the semipermeability of the side wall cytoplasm of the sieve tubes: (a) A series of samples taken from one tapping cut show a gradual decrease in concentration to a final value of about 70 % of that of the first sample. This is ascribed to an osmotic dilution with water from the surrounding tissue after the release of the sieve tube turgor. (b) The turgor of the sieve tubes is retained for one or two days after all the leaves have dropped in the fall. (c) There is no correlation between molecular size and gradient (no steeper gradients of substances with smaller molecules) which would suggest leaking of the sieve tubes.

2. A mass flow obviously does occur during about half an hour after tapping; the sieve plates are therefore permeable during this time. The sieve tubes immediately above the cut can be tapped by a second cut at any time after application of the first cut. This observation suggests that the permeability of the sieve plates is not an artifact.

3. The total molar concentration, undoubtedly a close measure of the turgor pressure gradient, is positive in the downward direction of the trunk throughout the summer. The gradients of the different substances are not the same, however. Therefore, in the fall, when the leaves form their abscission layer and cease supplying assimilates to the phloem, a gradient inversion of some of the substances takes place, and the total molar gradient disappears.

In agreement with other workers, the presented data suggest that there is a passive flow of solutes along a positive turgor gradient which is established and maintained by the metabolic entry of assimilates into and removal from the sieve tubes.

The author gratefully acknowledges his indebtedness to Professors K. V. Thimann and H. M. Raup for their interest in this work. Prof. Thimann gave most generously of his time for discussions and the critical consideration of the manuscript. Prof. Raup made available the laboratory facilities of the Harvard Forest and allowed the unlimited use of forest trees for experimental purposes.

Literature Cited

1. Bauer, L. Zur Frage der Stoffbewegungen in der Pflanze mit besonderer Berücksichtigung der Wanderung von Fluorochromen. Planta 42: 367–451. 1953.
2. Crafts, A. S. Further studies on exudation from cucurbits. Plant Physiol. 11: 63–79. 1936.
3. Crafts, A. S. and Lorenz, O. A. Composition of fruits and phloem exudate of cucurbits. Plant Physiol. 19: 326–337. 1944.
4. Currier, H. B., Esau, K. and Cheadle, V. I. Plasmolytic studies of phloem. Amer. Jour. Bot. 42: 68–81. 1955.
5. Esau, K. Plant Anatomy. Pp. 1–735. John Wiley & Sons, Inc., New York 1953.
6. Frey-Wyssling, A. Der Milchsafterguss von *Hevea brasiliensis* als Blutungserscheinung. Ein Beitrag zur Druckstromtheorie. Jahrb. wiss. Bot. 77: 560–626. 1933.
7. Hartig, Th. Beiträge zur physiologischen Forstbotanik. Allgem. Forst- und Jagztg. 36: 257–261. 1860.
8. Hartig, Th. Ueber die Bewegung des Saftes in den Holzpflanzen. Bot. Ztg. 19: 17–23. 1861.
9. Huber, B. Das Siebröhrensystem unserer Bäume und seine jahreszeitlichen Veränderungen. Jahrb. wiss. Bot. 88: 176–242. 1939.
10. Huber, B. Anatomical and physiological investigations on food translocation in trees. Intern. Symposium on Tree Physiol., Maria Moors Cabot Foundation, Publ. No. 4, Harvard University. (In press.)
11. Huber, B. Die Gewinnung von Eschenmanna—eine Nutzung von Siebröhrensaft. Ber. deut. bot. Ges. 66: 341–346. 1953.
12. Huber, B. and Rouschal, E. Anatomische und zellphysiologische Beobachtungen am Siebröhrensystem der Bäume. Ber. deut. bot. Ges. 56: 380–391. 1938.
13. Huber, B., Schmidt, E. and Jahnel, H. Untersuchungen über den Assimilatstrom. Tharandt. forst. Jahrb. 88: 1017–1050. 1937.
14. Kennedey, J. S. and Mittler, T. E. A method of obtaining phloem sap via the mouth-parts of aphids. Nature 171: 528. 1953.
15. Mittler, T. E. Amino-acids in phloem sap and their excretion by aphids. Nature 172: 207. 1953.
16. Mittler, T. E. The phloem sap supply to aphids feeding on willow trees. Intern. Symposium on Tree Physiol., Maria Moors Cabot Foundation, Publ. No. 4, Harvard University. (In press.)
17. Münch, E. Die Stoffbewegung in der Pflanze. Pp. 1–234. Gustav Fischer, Jena 1930.
18. Nelson, N. A photometric adaptation of the Somogyi method for the determination of glucose. Jour. Biol. Chem. 153: 375–380. 1944.
19. Röckl, B. Nachweis eines Konzentrationshubes zwischen Palisadenzellen und Siebröhren. Planta 36: 530–550. 1949.
20. Schumacher, W. Ueber die Plasmolysierbarkeit der Siebröhren. Jahrb. wiss. Bot. 88: 545–553. 1939.
21. Schumacher, W. and Hülsbruch, M. Zur Frage der Bewegung fluoreszierender Farbstoffe im Pflanzenkörper. Planta 45: 118–124. 1955.
22. Somogyi, M. A new reagent for the determination of sugars. Jour. Biol. Chem. 160: 61–68. 1945.
23. Tingley, M. A. Concentration gradients in plant exudates with reference to the mechanism of translocation. Amer. Jour. Bot. 31: 30–38. 1944.
24. Trevelyan, W. E., Procter, D. P. and Harrison, J. S. Detection of sugars on paper chromatograms. Nature 166: 444. 1950.
25. Wanner, H. Phosphataseverteilung und Kohlenhydrattansport in der Pflanze. Planta 41: 190–194. 1952.
26. Wanner, H. Die Zusammensetzung des Siebröhrensaftes: Kohlenhydrate. Ber. schweiz. bot. Ges. 63: 162–168. 1953.
27. Ziegler, H. Untersuchungen über die Leitung und Sekretion der Assimilate. Planta 47: 447–500. 1956.
28. Zimmermann, M. H. Translocation of organic substances in trees. I. The nature of the sugars in the sieve tube exudate of trees. Plant Physiol. 32: 288–291. 1957.
29. Zimmermann, M. H. Translocation of organic substances in the phloem of trees. Intern. Symposium on Tree Physiol., Maria Moors Cabot Foundation, Publ. No. 4, Harvard University. (In press.)

THE EFFECT OF SILICON ON YIELD AND MANGANESE-54 UPTAKE AND DISTRIBUTION IN THE LEAVES OF BARLEY PLANTS GROWN IN CULTURE SOLUTIONS[1]

D. EMERTON WILLIAMS and JAMES VLAMIS

Department of Soils and Plant Nutrition, University of California, Berkeley, California

Silicon in the form of its compounds occupies 87 % of the earth's crust and constitutes a large percentage of the ash of some plants grown in soil. The addition of silicon to culture solutions has been shown by a number of workers (2, 3, 5) to result in an increase in plant yield. In spite of its beneficial character, and the large amounts absorbed by plants, this element has not been shown to be essential to higher plants in the strict sense of the word. The beneficial effects obtained by the addition of silicon to culture solutions may well be due to secondary causes rather than to an essentiality on the part of silicon.

Previous work in this department by A. Ulrich (unpublished data) concerning the effect of silicon on yield and on the necrotic symptoms observed on the leaves of barley plants grown in culture solutions,

[1] Received revised manuscript March 19, 1957.