

cisions on the basis of the facts. County school boards can be set up on various bases, which will give the best results.

Some years ago I made the suggestion to the governor of one of our progressive states that every county in the state should be carrying on some kind of carefully controlled experiments to answer the problems of public administration, governmental organization, public health and education of that state. If the proper kind of arrangements were made, this could be done with relatively small expense. The results should be enormous in terms of human welfare. Every community in the state would know that it was a part of some broad social experiment attempting to give the answer to public problems. A great deal of volunteer effort of young people from school and other groups could be obtained. The time might easily come when a community would pride itself

more on the type of scientific experiments in the social field which are carried on than it would in its size or wealth.

It is quite true that we can not experiment in the social sciences in the narrow and rigid way that the laboratory scientist does, but we can experiment most usefully. The various parts of the Sloan experiment have thrown great light upon the problem of the effect of school instruction on changing food, clothing or housing in a low-income community. If the experiment is repeated in a great variety of forms and places, we should be able in a few generations to build up a far more accurate picture than any one now has of the effect of school instruction in changing a community. The experimental results available should make us very optimistic of the possibilities of extending scientific procedures into social problems. We can experiment in the social sciences with great profit to mankind.

TRANSLOCATION OF CARBOHYDRATES IN MAIZE¹

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It has been the aim of a large group of plant physiologists, with whom the writer likes to identify himself, to reduce the reactions and responses of living plants to processes demonstrable in our laboratory test-tubes. The evaporation of water from leaves, the absorption of water by roots and the diffusion of carbon dioxide through stomates are processes which we think we can soon, if not now, explain in terms of thermodynamics and the calculus. The tremendous strides of the last decade lead us to hope that we will be able eventually to explain photo-periodism, respiration and photosynthesis in terms of specific physico-chemical reactions. I think that we can see glimmerings of a similar basis for such vitalistic processes as protoplasm synthesis and the physiology of inheritance, but I confess myself baffled by some of the phenomena of translocation in plants.

The problem of the translocation of organic compounds in plants can be divided into the sub-problems of (a) the tissues concerned, (b) the compounds moved, (c) the mechanisms involved and (d) the controlling factors.

THE TISSUES CONCERNED

The experiments of Curtis² and of Mason³ are

¹ Address of the retiring president (1943) of the American Society of Plant Physiologists, presented at the Cleveland meeting of the American Association for the Advancement of Science, Cleveland, Ohio, September, 1944.

² O. F. Curtis, "The Translocation of Solutes in Plants." New York. 1935.

³ T. G. Mason and others. *Ann. Bot.*, 42: 189-253, 1928, and subsequent volumes.

generally considered to have established the phloem as the primary tissue of translocation. The maize plant with its many closed bundles is not adapted to studies of tissue function by ringing, etc., but we may assume that here, as in sumac, privet and cotton, the phloem is the important channel of food movement. The phloem of the stem, however, is surrounded by parenchyma and can not be studied separately. Our first task, therefore, has been to show that sugars are transferred between the phloem and the pith parenchyma, and that an analysis of the entire pith is capable of furnishing information on the progress of translocation. Such evidence has been obtained by covering plants growing in the field with light-tight covers and analyzing their tissues at intervals.

Typical data from one of these experiments are shown in Table 1. Ear shoot development was pro-

TABLE 1
CHANGES IN SUCROSE CONTENT OF TISSUES OF MAIZE PLANTS
HELD IN DARKNESS

Tissue and stage	Sucrose, percentage of green weight			
	At start	After 24 hours	After 72 hours	Loss
Leaves				
Tasseling	2.42	0.11	0.11	2.31
Milk	2.65	0.20	0.13	2.52
Milk-bagged ..	2.30	0.46	0.76	1.54
Stalks				
Tasseling	0.59	0.22	0.26	0.33
Milk	8.54	6.20	5.03	3.51
Milk-bagged ..	8.01	7.38	7.19	0.82
Shanks				
Milk	5.42	4.25	3.07	2.35
Milk-bagged ..	3.88	3.70	3.10	0.78
Cobs				
Milk	2.32	2.19	2.39	-0.07
Milk-bagged ..	2.36	1.55	1.34	1.02

ceeding rapidly at the tasseling stage but no grain was present. The milk stage was chosen, on the basis of previous experiments, to represent maximum translocation to the developing grain. A third series of plants was bagged to prevent pollination and grain development, and was then sampled on the same dates as the milk-stage plants. Changes in the sucrose content of the pithy stems and shanks were as great and almost as fast as the changes in the leaves. These changes, however, were dependent upon the presence of developing grain as a storage organ and were nearly absent in plants without grain.

At least a partial equilibrium between the sucrose content of the translocating tissues and of the much greater volume of pith is indicated. Such an equilibrium raises a morphological-physiological problem, for the two tissues are separated by the lignified cells of the bundle sheath. No parenchyma passages across this sheath, analogous to wood and phloem rays, have been observed or described. The more popular of the present theories of translocation assume that movement is normally restricted to living cells with plasmodesmal connections, and that little or no translocation would occur through tissues of the type surrounding the maize bundle.

THE COMPOUNDS MOVED

We assume that the carbohydrates translocated in the maize plant will be soluble or dispersable in the plant sap. Four compounds are available: fructose, glucose, sucrose and a part of the dextrin. The evidence here seems to be clearly in favor of sucrose. Nearly all the sugar and most of the carbohydrate of the leaf is sucrose. Sucrose losses clearly precede losses of other fractions, particularly of dextrans. In the stems sucrose is low in the growing plant but accumulates rapidly after tasseling until it constitutes 6 to 10 per cent. of the green weight of the pith. Overnight losses from the stalk are nearly pure sucrose, and sucrose is the only carbohydrate which consistently shows losses in darkness along the translocation pathway of leaves → sheaths → stalks → ear shanks (Table 2).

TABLE 2
CARBOHYDRATE LOSSES FROM TISSUES OF MAIZE PLANTS
HELD 24 HOURS IN DARKNESS. DATA ARE PER
CENT. OF GREEN WEIGHT

Tissue	Fructose	Glucose	Sucrose	Dextrin
Leaves	0.00	0.09	2.45	0.83
Sheaths	0.03	0.19	1.50	0.44
Stalks	-0.16	0.08	2.34	0.05
Shanks	0.00	-0.04	1.17	-0.10
Cobs	-0.04	0.01	0.13	0.52
Average	-0.03	0.07	1.52	0.35

The rapid initial losses of sucrose and the slower losses of dextrin suggest that the sugar is the trans-

location form and that the polysaccharide is moved after digestion. The data of Leonard⁴ should be recalled, however. He found that carbohydrate interconversion in maize leaves was so rapid that accumulation forms were not affected by the form supplied in the transpiration stream. Leaves injected with fructose accumulated both glucose and sucrose at the same rate as those injected with glucose. Such transformations may not be so rapid in the stem, however, and the evidence available indicates that sucrose is the important carbohydrate of translocation in maize.

THE MECHANISM OF TRANSLOCATION

Two mechanisms to explain translocation have been advanced. The Curtis-Mason hypothesis of accelerated diffusion along a positive gradient of the moving substance, with acceleration by protoplasmic streaming, interfacial movement or unknown factors, and the Muench hypothesis⁵ of mass flow on an osmotic gradient. Neither of these hypotheses is prepared to explain carbohydrate translocation in maize, where not only total but all individual gradients from leaves to stalks are negative by 2 to 50 or more times. Sucrose disappears from leaves containing 0.3 per cent. and moves through tissue containing 7 to 8 per cent. of the same sugar in at least partial equilibrium with the phloem. Glucose gradients may be nearly as steep and fructose concentrations in the stalks 200 times those in the leaves are not uncommon. The difficulty might be explained by a secretory action in the leaf—if that is an explanation—if it were not for evidence that such secretory, negative gradients are not only widespread throughout the plant, but that they show an interrelated polarization. We suggest that new hypotheses on the mechanism of translocation are needed.

POLARIZED TRANSLOCATION

Leonard's work from this laboratory on the polar export of sugars from the blade mesophyll of sugar beet⁴ was preceded by still unpublished work showing the same phenomena in maize. More recent work with maize and other plants has corroborated these findings, and Phyllis and Mason⁶ have shown a similar reaction in cotton. If mature sugar beets are darkened to prevent photosynthesis, the blade sugars are moved into the petiole and root, and the leaf blades die from lack of sugar while the roots contain 15 to 20 per cent. of sucrose. Young leaves on the same plant grow vigorously on this stored sugar. Apparently some change in the maturing phloem or

⁴ O. A. Leonard, *Am. Jour. Bot.*, 25: 78-83, 1938, and 26: 475-484, 1939.

⁵ A. S. Crafts, *Plant Physiol.*, 6: 1-41, 1931.

⁶ E. Phyllis and T. G. Mason, *Ann. Bot.*, 47: 585-634, 1933.

border parenchyma of the leaf eventually stops upward translocation. At the same time sugars are almost quantitatively exported from the blade against steep concentration gradients.

The reactions in maize are similar (*cf.* Table 1). Sucrose concentrations of 2 to 3 per cent. in the blade drop to 0.2 per cent. in 24 hours of darkness, while total sugar concentrations of 3 per cent. drop to 0.3 per cent. Removing or bagging the ears to prevent translocation to the grain gives a leaf drop of from 3 to 4 per cent. to 0.5 to 1.0 per cent. total sugars, showing some backing up into the leaf.

A reversed polarization shows in the cob where sterile (bagged) cobs show a drop in sugars after the plants are darkened, but fruiting cobs, from which sugars are being rapidly moved to the grain, may show sugar gains of 30 per cent. of their original concentration after 72 hours of darkness (*cf.* Table 1). A polarized movement toward the developing grain is indicated.

A still more striking demonstration of the polarizing action of developing grain may be obtained by removing all leaves from the main axis of a plant having well-developed basal branches or suckers. If these leaves are removed just before normal pollination, the ear shoot fails to develop and the stalk is barren. If the nearby leaves are left a few days until a polarizing action of the developing embryos can be established, full-sized ears can be produced by translocation from leaves on the sucker branches 8 or 10 feet from the ear. Typical data are shown in Table 3. No appreciable grain development, in

terms of dry weight, had occurred in the plants defoliated eight days after pollination. Polarization had been established, however, and normal grain was developed with food obtained from the leaves of the sucker stalks. Normal yields could be obtained with defoliation at the time of pollination by first bagging the ear shoots and holding the plants without defoliation until they had built up a local food reserve sufficient to initiate embryo development. All grain produced by the plants defoliated two days before pollination (-2) was on stalks held in this way. When the main stalk was defoliated just before the ear shoot emerged from the sheath, all further development of the shoot was prevented.

Unpublished and general evidence indicates that polarized translocation is a factor in many correlation and inhibition reactions of plants generally, as well as of maize.

SUMMARY

(1) The pith of maize shows a changing sugar content with changing sugar movement in the phloem which would not be predicted from our present picture of the morphology of the maize bundle.

(2) By all tests of changing concentration, sucrose is the important carbohydrate of translocation in maize. Interconversion of the several sugars is too rapid, however, to permit a final conclusion.

(3) An hypothesis of translocation in maize must not only account for movement against an osmotic gradient, but against gradients of each of the substances which might possibly be translocated. Such secretory translocation certainly occurs between the leaf mesophyll and the phloem and probably along the phloem itself.

(4) Translocation in maize is polarized, out of the leaf, out of the xylem and toward the developing fruit. Polarized translocation out of the leaf is established during the later stages of tissue differentiation. Polarized translocation toward the fruit is established in the early phases of embryo development and does not develop in the absence of pollination.

TABLE 3

YIELDS OF MAIZE PLANTS WITH BASAL BRANCHES WHEN THE MAIN STALK WAS DEFOLIATED BEFORE AND AFTER POLLINATION

Defoliation—days after pollination						
-2	0	1	2	4	8	Ck
Yield as a percentage of check						
10.9	34.4	48.7	59.0	73.7	99.5	100.0

OBITUARY

RECENT DEATHS

DR. THOMAS F. HOLGATE, professor emeritus of mathematics and dean emeritus of the School of Liberal Arts of Northwestern University, died on April 11. He was eighty-six years old.

ALFRED VICTOR DE FOREST, professor of mechanical engineering at the Massachusetts Institute of Technology and president of the Magnaflux Corporation, died on April 5 at the age of fifty-six years.

DR. RAYMOND HASKELL, consulting engineer for the Texas Oil Company, died on April 6. He was sixty-six years old.

SIR WILLIAM NAPIER SHAW, F.R.S., meteorologist, a former director of the British Meteorological Office, died on March 23 at the age of ninety-one years.

DR. HANS FISCHER, professor of organic chemistry at the Technical High School at Munich, has died at the age of sixty-three years.