ratio in ion absorption experiments. Plant Physiol. 36: 62–65.
16. KAHN, J. S. AND J. B. HANSON. 1957. The effect of calcium on potassium accumulation in corn and soybean roots. Plant Physiol. 32: 312–16.
17. LOWRY, O. H., N. J. ROSEBROUGH, A. L. FARR, AND R. J. RANDALL. 1951. Protein measurement with the Folin-phenol reagent. J. Biol. Chem. 193: 265–75.
18. MACDONALD, I. R. AND G. G. LATIES. 1963. Kinetic studies on anion absorption by potato slices at OC. Plant Physiol. 38: 38–44.
19. MARINOS, N. G. 1962. Studies on submicroscopic aspects of mineral deficiencies. I. Calcium deficiency in the shoot apex of barley. Am. J. Botany 49: 834–41.
20. TANADA, T. 1955. Effects of ultraviolet radiation and calcium and their interaction on salt absorption by excised mung bean roots. Plant Physiol. 30: 221–25.
21. TANADA, T. 1956. Effect of ribonuclease on salt absorption by excised mung bean roots. Plant Physiol. 31: 251–53.
22. TANADA, T. 1956. Effect of sulfhydrl inhibitors on rubidium absorption by excised mung bean roots. Plant Physiol. 31: 403–06.
23. TANADA, T. 1962. Localization and mechanism of calcium stimulation of rubidium absorption in the mung bean root. Am. J. Botany 49: 1068–72.
24. VASINGTON, F. D. AND J. V. MURPHY. 1962. Ca^{++} uptake by rat kidney mitochondria and its dependence on respiration and phosphorylation. J. Biol. Chem. 237: 2670–77.
25. VIETS, F. G. 1944. Calcium and other polyvalent cations as accelerators of ion accumulation by excised barley roots. Plant Physiol. 19: 466–80.
26. WAISEL, Y. 1962. The effect of Ca on the uptake of monovalent ions by excised barley roots. Physiol. Plantarum 15: 709–24.

Sugar Gradients and Translocation of Sucrose in Detached Blades of Sugarcane [1, 2]

Constance E. Hartt and Hugo P. Kortschak

Physiology and Biochemistry Department, Experiment Station, Hawaiian Sugar Planters' Association, Honolulu, Hawaii

Studies of the translocation of C^{14}-photosynthate in entire plants of sugarcane grown under normal conditions of climate and nutrition have been summarized (12). Another paper (11) reports defoliation tests which indicated that a major force in translocation resides within the leaf. The present paper describes experiments with detached blades which were started in 1960 (9). Harvesting and processing entire plants of sugarcane involve considerable time and work. This study with detached blades was undertaken to simplify the translocation system and to speed the investigation of the mechanism of translocation in sugarcane.

Materials and Methods

Two varieties were used in these studies: H37-1933 (a complex interspecific hybrid involving *Saccharum officinarum* L., *S. spontaneum* L., and *S. robustum* Brandes and Jeswiet ex Grassl.) and H50-7209 (a hybrid involving *S. officinarum* L., *S. spontaneum* L., and possibly others). The blades were taken from plants grown in the field at the Experiment Station.

Blades were cut from the plants and immediately recut twice under water, then taken to the photosynthesis room, transferred under water to jars containing water, and preilluminated at 2000 ft-c for at least 10 minutes. Preliminary tests indicated that blades cut from the plant and fed $C^{14}O_2$ at a uniform, moderate intensity of light gave better results than plants fed outdoors, at high intensities of light, attached to the plant. High intensities of light, e.g. 8,000 ft-c. decreased translocation in detached blades.

The methods used in the studies reported herein were the same as those reported previously (12), except that the blade was detached from the plant before being fed $C^{14}O_2$. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade for 5 minutes at 2000 ft-c, using the chamber described previously (12). All treatments were initiated immediately after removing the feeding chamber. After translocation, the blade was cut into sections, dried, weighed, milled, and counted at infinite thickness.

C^{14} results are expressed as: relative specific activity, which is the net count per minute as infinite thickness; as relative total counts, which is the relative

[1] Sept. 9, 1963.
[2] Published with the approval of the Director as Paper No. 139 of the Journal Series of the Experiment Station. Hawaiian Sugar Planters' Association.

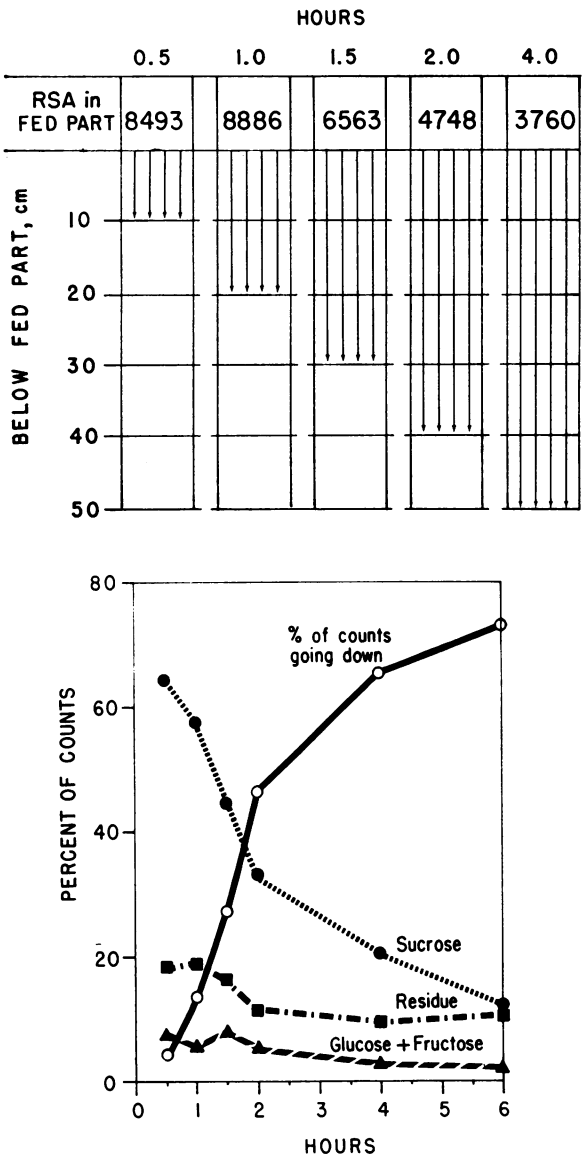

FIG. 1. Translocation in detached blades at 2000 ft-c for 0.5 to 6 hours. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade at a position 50 cm above the cut base, for 5 minutes at 2000 ft-c. A (*upper*). Relative specific activity (RSA) in the fed part decreased with time. Arrows point to the lowest position on the blade having a relative specific activity of 500 or more cpm. B (*lower*). Total translocation is expressed as % of counts going down the blade. Insoluble residue and chromatographically identified sucrose and glucose plus fructose are expressed as % of C^{14} remaining in the fed part.

specific activity times the total dry weight in milligrams; and as percentage of relative total counts in the blade. Relative total counts in the blade is obtained by adding the relative total counts of each part. When calculated to infinite thinness, results are expressed as total counts.

Absorption of P^{32} from dilute aqueous solution was studied to determine its polarity. P^{32} results are expressed as net count.

Table I

Translocation at 2000 ft-c

Relative specific activity at 1, 4, and 6 hours. 10 μc of $C^{14}O_2$ was fed to a 20-cm length of blade at a position 50 cm above the cut base for 5 minutes at 2000 ft-c.

Part	Hours		
	1.0	4.0	6.0
	cpm	cpm	cpm
Apex, 10 cm and above	17	27	21
10 cm above fed part	22	14	24
Fed part (20 cm)	8886	3760	3080
cm below fed part-10	1751	3113	2823
20	740	3251	3571
30	140	3395	3443
40	0	2787	3375
50	0	631	1356

Results

Translocation Takes Place in Detached Blades. Translocation in similar blades for 0.5 to 4 hours at 2000 ft-c is demonstrated in figure 1A, in which the arrows point to the lowest position on the blade having a relative specific activity of 500 or more cpm. As translocation took place, the relative specific activity of the fed part decreased and a gradient in radioactivity was established (table I). For the first 4 hours the fed part had the highest activity, but at 6 hours some basal sections had higher activities, illustrating accumulation. Each basal section being 10 cm long, the velocity calculated at the center of the third section (table I, 1 hr) was 25 cm/hr, or 0.4 cm/min. This is slower than in attached blades, where the rate ranged from 0.7 to over 2 cm/min (12).

Values for relative specific activity at 1, 4, and 6 hours (table I) show that major transport was basipetal. The low activity in the apex was not changed by time and probably represented leakage of $C^{14}O_2$ into intercellular spaces during feeding. Small but definite counts could be found in the apex even after feeding in total darkness (table II).

Table II

Dark Translocation after Dark Feeding

20 μc of $C^{14}O_2$ was fed to a 20-cm central part of a blade for 10 minutes in total darkness. Translocation time was 24 hours in total darkness.

Part of blade	Relative specific activity cpm
Apex, upper half	8
Apex, lower half	8
Fed part	55
Base, upper half	0
Base, lower half	0

Table III

Composition of Apex and Base after Translocation for 24 Hours

Dosage, time, and position of feeding were as in table I. The blades in the light received 2000 ft-c all day but were in darkness from 4 P.M. to 8 A.M. The blades in the dark were wrapped in aluminum foil. Milled parts were extracted with 80% ethanol. Percentage of counts in residue and chromatographically separated components showed that sucrose had the highest percentage of radioactivity.

Component	2000 ft-c*		Entire blade dark**
	Apex (All)	Base (20 cm below fed part)	Apex (10 cm above fed part)
	%	%	%
Sucrose	79	71.5	79.5
Glucose	3	3.2	3.9
Fructose	4	4.1	3.5
Insoluble residue	6	14.6	5.2
Other	7	6.4	8.0

* For distribution of counts in the blade see figure 7, the left control blade.

** For distribution of counts in the blade see figure 12, the left darkened blade.

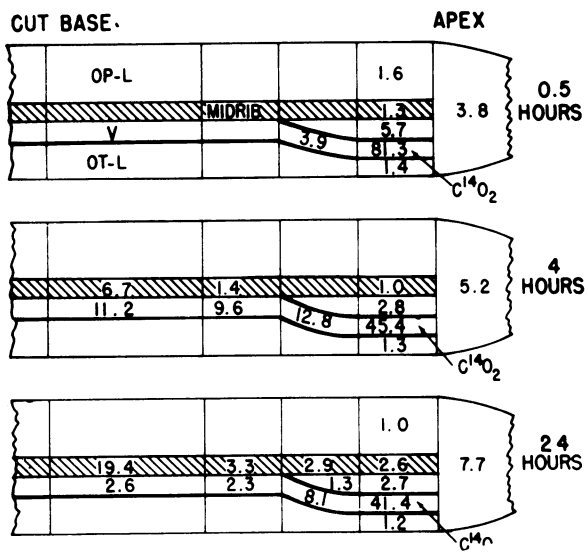

FIG. 2. Labeled photosynthate follows the veins to the midrib. % of C^{14} in each part 0.5 to 24 hours after feeding 30 μc of $C^{14}O_2$ for 3 minutes at 2000 ft-c, using the 6.5-ml chamber, to small areas indicated by arrows. Parts having less than 1% of C^{14} are blank. Strip below fed part torn down by hand at harvest, following veins. OP-L, opposite lamina; V, veins below fed part; OT-L, outer lamina. Translocation at 2000 ft-c for 0.5 hours, 4 hours, and until 4 PM and after 8 AM for the 24-hour blade. The 24-hour blade was in darkness from 4 PM until 8 AM. Total counts × 10^5: 0.5 hours, 2.4; 4 hours, 1.4; 24 hours, 2.2.

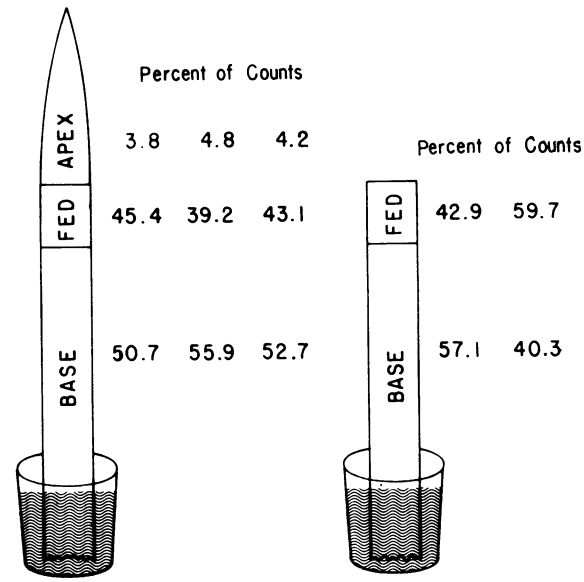

FIG. 3. Translocation in detached blades was not affected by cutting off the apex. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade for 5 minutes at 2000 ft-c. Left: 3 controls. Right: 2 blades with the apex cut off at the upper edge of the fed part immediately after removing the feeding chamber. Total translocation time, 24 hours. 2000 ft-c by day; lights off from 4 PM to 8 AM. Relative total counts × 10^6: Controls, 20.2, 10.9, 7.3; apex cut, 23.4, 16.1.

The percentage of isotope going down the blade increased rapidly the first 2 hours (fig 1B), after which the increase was slower, probably due to the accumulation of radioactive compounds in basal sections (table I, 6 hr).

Only a trace of radioactivity was detected in the water (11). Aronoff (1) also noted the absence of activity in the nutrient solution or water in which the petiole of a fed blade stood.

The chief constituent decreasing in the fed part was sucrose, counted after separation by paper chromatography (fig 1B). Insoluble residue also decreased the first 2 hours. Sucrose was also the chief constitutent found in the apex and in the base after translocation at 2000 ft-c (table III).

When only a small spot on one lamina was fed $C^{14}O_2$ (fig 2), radioactive sucrose followed the veins below the fed part to the midrib, where it accumulated to 7% of the counts in the blade in 4 hours and to 19% in 24 hours. At 24 hours, 90% of the counts in the lower midrib were still soluble in alcohol, and 98.4% of the counts in the extract were sucrose. There were no other significant counts in the extract.

These experiments show that translocation of C^{14}-photosynthate takes place in detached blades and resembles translocation in attached blades (12) in these respects: A) the translocate follows the veins to the midrib; B) major transport is basipetal; and C) the principal and perhaps the only compound moving is sucrose.

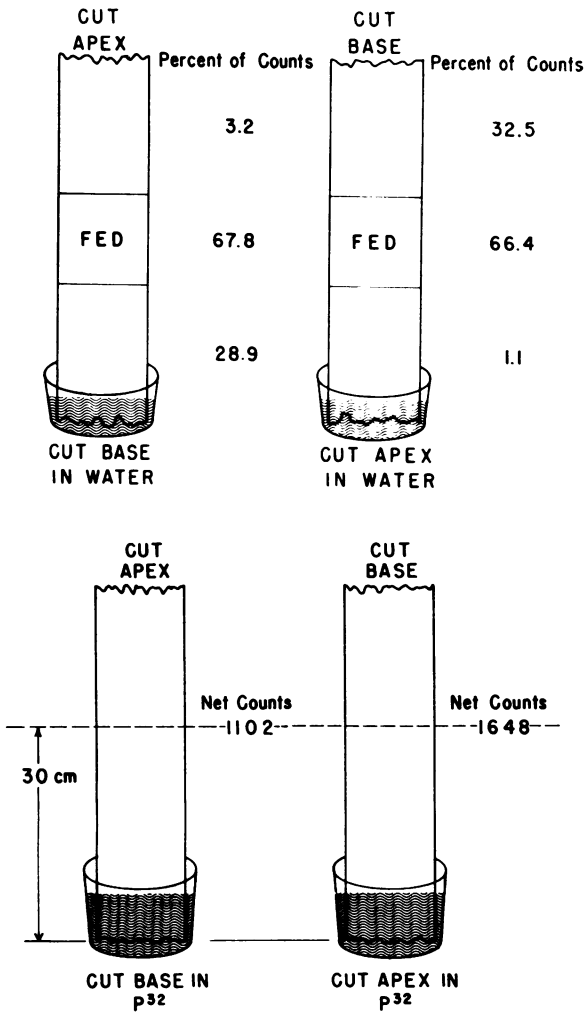

FIG. 4, 5. Polarity in translocation of C^{14} and absence of polarity in absorption of P^{32}. FIG. 4 (*upper*). Translocation of C^{14} at 2000 ft-c (dark at night) was more to the base than to the apex regardless of the position of the blade. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of entire blade at a position 30 cm above the cut base, for 5 minutes at 2000 ft-c. The apex was then cut off 30 cm above the fed part. The apex of the blade at right was cut under water. Translocation time, 22 hours. Relative total counts × 10^6: upright blade (left), 5.8; upside down blade (right), 7.6. FIG. 5 (*lower*). Absorption of P^{32} from a dilute solution for 30 minutes at 4000 ft-c by cut base (left) or cut apex (right). Carrier-free P^{32} (Oak Ridge) was added to tap water and used with no other addition, at the pH of tap water (approximately pH 6.2).

Presence or Absence of Apex. Contrary to our results with attached blades (11) translocation in detached blades was not affected by cutting off the apex just above the fed part (fig 3). This is because the detached blade has no other blades to compete with, while the attached blade must compete with the streams of photosynthate coming down from the leaves above it and cannot compete when a large part of its apex has been removed. Since cutting off the apex of a detached blade has no effect on translocation in the blade, it is not necessary to use an entire blade to study the process of translocation.

Polarity of C^{14} Translocation vs P^{32} Absorption. A blade that had just been fed $C^{14}O_2$ while standing upright with its cut base in a jar of water was held in a horizontal position. With the base kept in the jar of water, more than 30 cm of the apex was immersed in a pan of water while the blade was cut off 30 cm above the fed part, after which the base was removed from water. The blade was then standing upside down in water. Translocation took place at 2000 ft-c with the cut apex standing in water and the cut base up in the air. C^{14} moved principally toward the morphological base of the blade regardless of the position of the blade (fig 4). These results demonstrate a polarity in translocation of C^{14}-photosynthate not affected by position of the blade and independent of a connection with the stalk.

To determine if a similar polarity operates in the xylem, blades were stood upright or upside down in tap water labeled with P^{32}. The P^{32} was absorbed and moved upward regardless of orientation of the blade (fig 5), since movement in the xylem is a pull by transpiration. After absorption of P^{32} for 30 minutes, the net count in the upside down blade was even stronger than in the upright blade.

These results demonstrate that translocation of C^{14}-photosynthate, a process which is conceded to take place in the phloem (25), exhibits polarity.

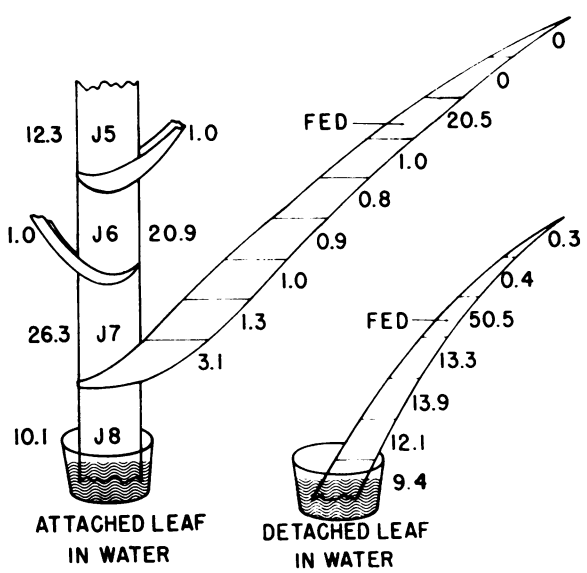

FIG. 6. A 4-joint length of stem provided a sink and increased the percentage of translocation from the fed part. $C^{14}O_2$ (10 μc) was fed at the position indicated, after detachment from the plant, for 5 minutes in sun (7000 to 8000 ft-c). Translocation time was 48 hours in the greenhouse, with normal variation in light. J5, J6, J7, and J8 indicate the number of the joint, counting from the top downward, the joint bearing the spindle (unrolled leaf) being designated No. 1. Results are presented as % of relative total counts. Relative total counts × 10^6: attached (left), 3.3; detached (right), 3.7.

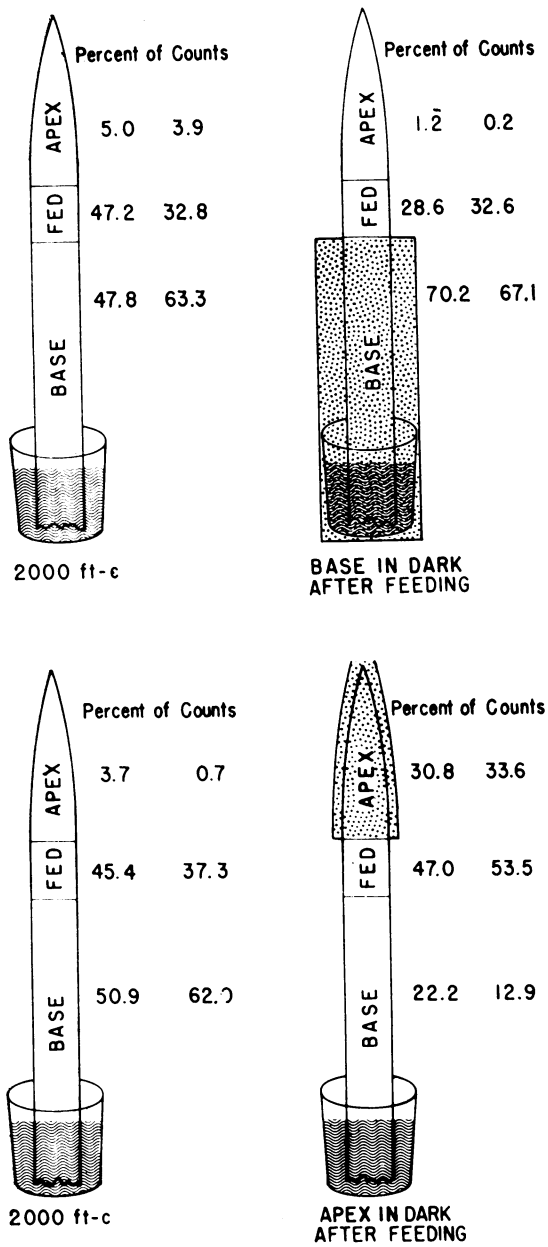

FIG. 7, 8. A darkened base or apex acts as a sink. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade at a position 50 cm above the cut base, for 5 minutes at 2000 ft-c. Immediately after removing the feeding chamber, the base (fig 7) or apex (fig 8) was wrapped in aluminum foil. Experiments were conducted in duplicate. FIG. 7 (*upper*). Darkening the base decreased acropetal and increased basipetal translocation. Translocation time, 24 hours; 2000 ft-c by day, lights off from 4 PM to 8 AM Relative total counts × 10^6: controls (left) 6.1, 3.2; 2 blades with bases wrapped in foil (right) 6.5, 8.1. For chromatography of the control at left, see table III. FIG. 8 (*lower*). Darkening the apex increased acropetal and decreased basipetal translocation. Translocation time, 6 hours, at 2000 ft-c. Relative total counts × 10^6: controls (left) 8.5, 7.5; 2 blades with apices wrapped in foil (right) 8.1, 5.4.

Table IV

Composition of Apex and Base after Translocation for 6 Hours, Comparing Translocation to Base (2000 ft-c, 6 hours) and Translocation to Apex (fed part plus apex dark, 6 hours)

Dosage, time, and position of feeding were as in table I. Blades No. 1 and 4 were completely lighted. Blades No. 2 and 5 received light on the basal parts only, the fed part plus apex being wrapped in aluminum foil immediately after removing the feeding chamber, (fig. 10). Milled parts were extracted with 80 % ethanol. Chromatographically separated sucrose had the highest percentage of radioactivity.

Component	Control in light		Fed part + apex dark	
	Section B_2*		Section A_2**	
	Blade No. 1	4	2	5
	%	%	%	%
Sucrose	76.6	75.2	75.8	70.7
Glucose	2.8	2.4	4.3	4.1
Fructose	3.4	2.9	4.5	4.1
Phosphates + amino acids	2.7	2.3	2.9	4.7
Insoluble residue	13.5	16.2	10.6	14.3

* 10 to 20 cm below fed part.
** 10 cm above fed part to tip of apex.

Since the absorption of water labeled with P^{32}, a process which is conceded to take place in the xylem, exhibits no polarity, a simple experimental distinction can be made between solutes moving in the transpiration stream and solutes moving in the phloem.

A Sink Increases Translocation. Translocation of photosynthate in the light does not require a sink, i.e. a place removing sugar from the translocation system by using it. The entire blade is green, is exposed to light and is presumably conducting photosynthesis, yet C^{14} fixed in the fed part goes down the blade. But a sink does increase the amount of translocation, as shown when the leaf was attached to a short length of stem (fig 6).

Effect of Darkening Parts of the Blade after Removing the Feeding Chamber. When the base of the blade was wrapped in aluminum foil, fewer counts went to the apex, and more to the base, than in the control (fig 7). Thus the darkened base acted as a a sink. Darkening the apex also provided a sink, greatly increasing the percentage of counts moving above the fed part, as well as decreasing basipetal transport by competition (fig 8). Darkening only the fed part curtailed translocation to the base but had no significant effect upon translocation to the apex (fig 9). When both the apex and the fed part were darkened, total translocation was decreased (fig 10). Basipetal translocation was almost completely inhibited, most of the counts that moved going to the apex. Counts in the base of the control blades and in the apex of the blades with fed part plus apex darkened were over 70 % sucrose (table IV). Conversion of sucrose to other components had also taken place, especially to insoluble residue.

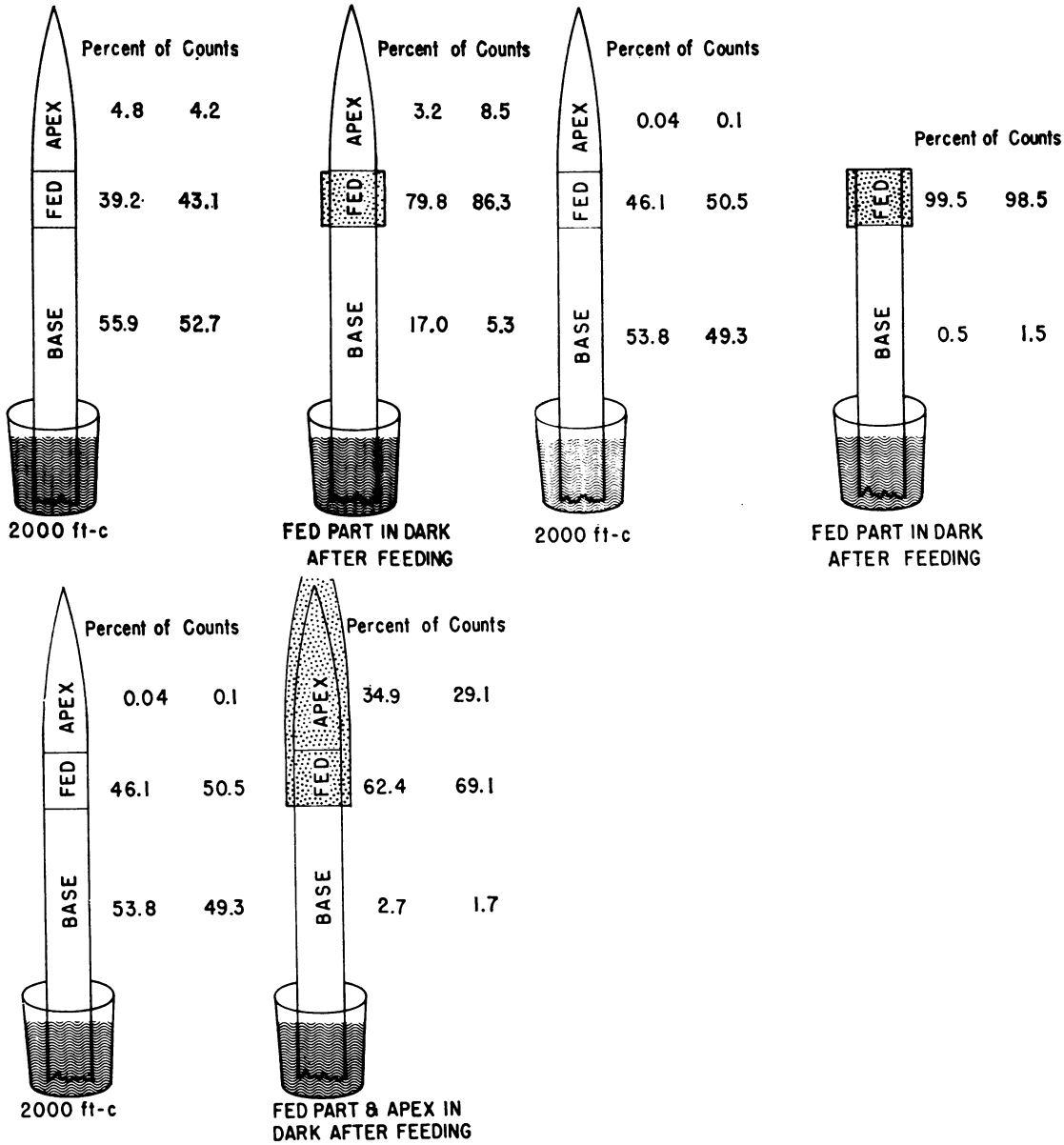

FIG. 9, 10, 11. Darkening the fed part decreased translocation therefrom, the amount of the decrease depending upon whether or not the apex is also darkened or cut off. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade at a position 50 cm above the cut base for 5 minutes at 2000 ft-c. Immediately after removing the feeding chamber, the fed part (figs 9, 11) or fed part plus apex (fig 10) was wrapped in aluminum foil. In addition, the apices were cut from the blades at the right (fig 11). Experiments were conducted in duplicate. FIG. 9 (*upper left*). Darkening the fed part decreased basipetal translocation but had no effect on acropetal translocation. Translocation time, 24 hours; 2000 ft-c by day, lights off from 4 PM to 8 AM. Relative total counts × 10^6: controls (left), 10.9, 7.3; fed part dark (right), 5.2, 4.2. FIG. 10 (*lower left*). Darkening the apex and the fed part increased acropetal and decreased basipetal translocation. Translocation time: 6 hours at 2000 ft-c. Relative total counts × 10^6: controls (left) 21.3, 15.6; fed part plus apex dark (right) 9.2, 8.9. For chromatography see table IV. FIG. 11 (*upper right*). Darkening the fed part, with the apex cut off, almost completely inhibited translocation. Translocation time; 6 hours at 2000 ft-c. Relative total counts × 10^6: controls (left) 21.3, 15.6; fed part dark and apex cut off (right) 9.0, 8.6. For chromatography of the fed part see table V.

Darkening the fed part, with the apex cut off, almost completely inhibited translocation (fig 11). Chromatography of the fed part (table V) showed the presence of sucrose counts, so it was not the lack of sucrose which prevented translocation.

Effect of Darkening or Cutting on Total Counts in the Entire Blade. Although dosage of $C^{14}O_2$ for each blade was 10 μc, differences were noted in relative total counts (table VI). Cutting off the apex had no significant effect on the relative total counts

Table V

Composition of the Fed Part after Translocation for 6 hours

Dosage, time, and position of feeding were as in table I. The control blades were completely lighted (2000 ft-c). The other blades were lighted on the basal parts only, the fed part being wrapped in aluminum foil and the apex cut off immediately after removing the feeding chamber (fig 11). Milled parts were extracted with 80% ethanol. Insoluble residue and chromatographically separated sucrose had the highest percentages of radioactivity.

Component	Controls in light		Fed part dark and apex cut	
Sucrose	36.2	39.3	41.1	43.3
Glucose	2.7	1.7	3.0	2.9
Fructose	3.3	2.5	4.4	3.9
Phosphates + amino acids	2.5	2.7	7.7	7.1
Insoluble residue	53.1	50.8	35.8	33.3

in the entire blade. Darkening the apex only or the base only gave no decrease. But whenever the fed part was darkened, either alone or with the apex or base or entire blade dark, the relative total counts were cut approximately in half.

Therefore, darkening the fed part right after feeding decreased the total radioactivity. Darkening the fed part either prevented completion of fixation into stable compounds, or increased respiratory use of C^{14} compounds, or both. The fact that darkening the fed part increased the percentage of counts in the fraction "organic phosphates plus amino acids" (table V) favors the suggestion that the decrease in relative total counts was due to increased respiration in the dark, since many respiratory intermediates are organic phosphate compounds. If so, this means that an increase in respiration is associated with a decrease in translocation, i.e. respiration competes with translocation for the newly-labeled sucrose. Definite evidence of the respiratory release of $C^{14}O_2$ soon after fixation has been presented by Nishida (22) for cut leaves of rice, barley, and Hydrangea.

Table VI

Effect of Cutting off Apex or Darkening Parts of Blades on the Relative Total Counts in Entire Blades

The relative total counts in duplicate treated blades were averaged and compared with the average of 2 control blades. The difference was calculated as percentage. (+, a gain due to treatment; —, a loss due to treatment). There was a significant decrease in total radioactivity only when the fed part was darkened after feeding.

Treatment	% change in relative total counts
Cutting off apex	0
Darkening apex only	— 12*
Darkening base only	+ 40
Fed part dark	— 44
Fed part + apex dark	— 50
Fed part dark, apex cut off	— 50
Fed part dark, apex cut off	— 45
Fed part + base dark	— 50
Entire blade dark	— 55
Entire blade dark	— 50

* Not significant.

Effect of Darkening the Entire Blade. Morning Blades Cut at 8:20 AM. When the entire blade was covered with foil, the percentage of counts leaving the fed part was reduced and the direction of translocation was reversed (fig 12). This effect of light or darkness on the entire blade was not due merely to initial sucrose gradients, because initial sucrose gradients in the blades should be the same. Neither was it due to a sink, for when the entire blade was dark the entire blade should be a sink. Yet the counts, chromatographically identified as sucrose (table III), went primarily upward to the apex. In this test, with blades cut at 8:20 AM, darkness reversed polarity.

Polarity of Translocation in the Dark. Translocation to the apex of darkened blades was at first considered to be due to a leakage of sucrose into the xylem followed by the upward pull of transpiration. But in a test with cut base or cut apex in water, both in the dark after feeding, radioactive sucrose went chiefly to the apex regardless of orientation of the blade (fig 13). Thus acropetal translocation in the dark, like basipetal translocation in the light, exhibits polarity not affected by gravity, position, or the pull of transpiration. Since acropetal transloca-

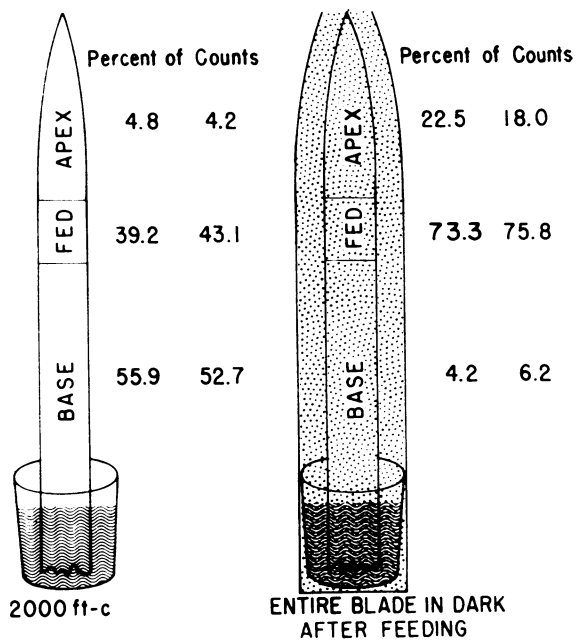

FIG. 12. Darkening the entire blade decreased basipetal and increased acropetal translocation. Blades were cut in the field at 8:20 AM $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade at a position 50 cm above the cut base, for 5 minutes at 2000 ft-c. Translocation time, 24 hours; 2000 ft-c by day, dark at night. Relative total counts × 10^6 controls (left) 10.9, 7.3; entire blade dark (right) 5.6, 3.2. For chromatography of the apex of the left darkened blade, see table III.

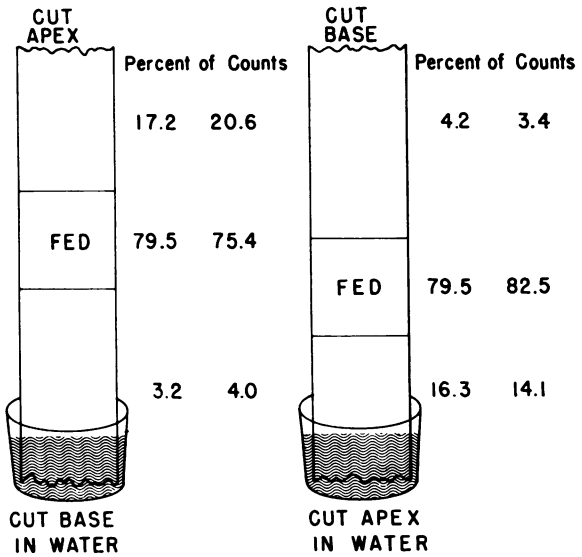

FIG. 13. Translocation for 24 hours in a dark room was more to the apex than to the base regardless of position of the blade. Blades were cut in the field at 8:20 AM. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade at a position 40 cm above the cut base. The apex was cut off 30 cm above the fed part. The blades at right were cut under water. All blades were placed in the dark immediately after feeding. Relative total counts × 10^6: left (upright blades) 3.2, 4.2; right (upside down blades) 4.0, 4.4.

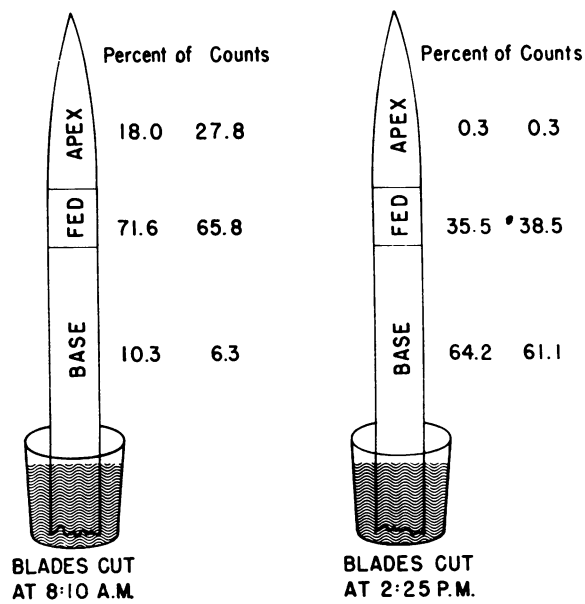

FIG. 14. Morning and afternoon blades differ in ability to translocate in the dark. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade for 5 minutes at 2000 ft-c. Blades were placed in the dark immediately after feeding. Left, 2 morning blades, translocation time, 24 hours. Right, 2 afternoon blades, translocation time, 18 hours. Relative total counts × 10^6: Morning blades (left) 3.2, 4.3; afternoon blades (right) 6.0, 6.0.

Table VII

Effect of Time of Day on Sucrose Gradients

Sucrose percentages in blades cut in the morning and in the afternoon, showing strong positive gradients in sucrose in the afternoon blades.

	Sucrose as % fr wt			
	Cut before 8:30 AM		Cut 2:00–2:30 PM	
cm above cut base	Blade 1	Blade 2	Blade 3	Blade 4
100 and above	0.708	0.985	2.537	2.314
80–100	0.772	0.831	2.379	2.495
60–80	0.625	0.746	1.719	2.308
40–60	0.736	0.656	1.340	1.793
20–40	0.671	0.628	1.103	1.473
0–20	0.650	0.656	0.885	1.318

tion in the dark is unaffected by the pull of transpiration, thus resembling basipetal translocation in the light and differing from the absorption of water labeled with P^{32}, acropetal translocation in the dark is now considered to take place in the phloem. If this is true, then it follows that even in the dark the requirements for entering the phloem are present, and a force for translocation is present, but the factor governing direction of translocation within the sieve tube of the blade is changed.

Translocation in the Dark Depends on Time of Day. Although blades cut in the field soon after 8:00 AM showed less total translocation in the dark than in the light (fig 12), blades taken from the same plot in the afternoon could translocate very well in total darkness (fig 14). Blades cut at intervals during the day gradually increased in ability to translocate in the dark. But blades cut at 8:15 AM and kept in the light until 2:00 PM before being fed $C^{14}O_2$, did not increase in ability to translocate in the dark. To develop this ability the leaf must be attached to the plant.

These findings can be explained in part by sucrose gradients in the blades (table VII). Blades cut in the early morning have little or no difference in sucrose percentage along their length. Blades cut in the afternoon, however, have a definite positive gradient in sucrose, the apex having twice as much sucrose as the base. Leaves cut in the morning and exposed to light all day can increase in percentage of sucrose but cannot develop a positive gradient, since the sucrose moves down toward the cut end and accumulates.

The results in table VII and figure 14 were obtained using different blades for counting and for analysis. The results were confirmed by using the same blades for measuring translocation in the dark, as well as for initial and final sucrose gradients, by the half-leaf method (table VIII). Translocation in the dark in the morning blade was more to the apex than to the base, but primarily to the base in the afternoon blade. Initial sucrose gradient in the afternoon blade was considerably stronger than in the morning blade. The loss in sucrose by both blades

Table VIII

Initial and Final Sucrose Gradients in AM and PM Blades, and Translocation in the Dark

Blade No. 5 was cut from the plant and recut under water. The apex was cut off at 100 cm and discarded. The 100-cm length of blade was preilluminated for 10 minutes at 2000 ft-c. A dose of 10 μc of $C^{14}O_2$ was fed to the central section (40–60 cm from the base) for 5 minutes at 2000 ft-c. Immediately after removing the feeding chamber, the right (initial) lamina was cut from the midrib and divided into the initial parts: apex, fed, base. The parts were weighed, killed, and extracted in ethanol, counted and analyzed. The left (final) lamina, still attached to the midrib and standing in water, was placed in the dark for 24 hours, after which it was treated the same way as the initial lamina. The midrib was subdivided and its counts added to those of the final lamina.

Part of Blade	Length cm	Sucrose as % fr wt		% of total counts before and after translocation for 24 hr in the dark	
		Initial lamina	Final lamina	Before	After*
		Blade cut at 8:30 AM			
Apex	60–100	0.52	0.37	0.6	14.7
Fed	40–60	0.53**	0.32	98.9	73.6
Base	0–40	0.50	0.36	0.5	11.7
				TC × 10^4 19.2	9.5
		Blade cut at 2:30 PM			
Apex	60–100	1.35	0.47	0.0	1.7
Fed	40–60	1.16**	0.59	99.8	61.0
Base	0–40	0.90	0.90	0.2	37.3
				TC × 10^4 9.1	6.9

* Includes midrib.

** For chromatography of initial fed parts, see table IX.

during the 24 hours in the dark is attributed to respiration and conversion to other components. Final sucrose percentages in the morning blade were nearly uniform, but in the afternoon blade a definite negative gradient in sucrose percentage had developed. Thus, a positive gradient in sucrose is a requirement for initiation of translocation in the dark.

Table VIII shows clearly that the translocation pool and the gradient pool are identical. The gradient in percentage of sucrose in the morning blade did not change on standing for 24 hours in darkness, while in the afternoon blade the initial positive gradient was changed to a final negative gradient. The translocation gradient labled with C^{14}, reflected the sucrose gradient determined by analysis.

Table IX

Chromatography of Initial Fed Parts of AM and PM Blades

Same leaves as in table VIII.

Component	% of total counts	
	AM blade	PM blade
Sucrose	30.1	30.7
Glucose	7.4	9.4
Fructose	9.0	9.3
Unknown*	4.8	3.9
Phosphoglyceric acid	4.0	3.4
Hexose phosphate	2.2	1.1
Aspartic acid	3.5	2.9
Malic acid	18.6	13.9
Insoluble residue	7.5	14.4
Undetermined	12.9	11.0

* Component between sucrose and glucose.

All blades so far studied which were cut in the early morning, i.e. up to approximately 8:30, gave much less total translocation in the dark than in the light, and more acropetal translocation in the dark than in the light. But not all morning blades have translocated more acropetally than basipetally in the dark. The total number of control blades cut by 8:30 AM and allowed to translocate in the dark for 6 to 24 hours is 49. Thirty-four translocated more to the apex than to the base; 15 more to the base than to the apex. Sugar analyses were not performed. Possibly some of the 15 blades had initial positive gradients in sucrose. There may also be other differences in the blades.

As translocation proceeds, sugar (both radioactive and nonradioactive) accumulates in the basal sections, and a factor must be found which can push the sugar down against the gradient. An attempt was made to find the unknown factor by chromatographing extracts of the initial fed parts of the same blades as in table VIII. The only major differences were a higher percentage of counts in malic acid in the morning blade, and a higher percentage in insoluble residue in the afternoon blade (table IX). Both blades had the same percentage of counts in sucrose. Insoluble residue may contain the factor, since residue counts are converted to sucrose during the night, a process which enables translocation to continue in an attached blade (10).

The unkown regulating factor is developed in the light, for any normal morning leaf can translocate in the light, irrespective of initial sucrose gradient.

Absorption of Sugar by Cut Base or Apex. Since detached blades can translocate normally in the dark only when they have a sharp initial sucrose gradient,

Table X

Effect of Standing Cut Base of Blade in 2.5 % (73 m M/liter) Sucrose upon Translocation in Light or Darkness

Blades were detached from the plant, recut under water, and transferred to pint jars of tap water. Jars containing blades destined to stand in sucrose contained exactly 100 ml of tap water. 100 ml of double strength sucrose was then added to the jar and mixed with the tap water, care being taken not to expose the cut base of the blade to air. After preillumination at 2000 ft-c, 10 μc of $C^{14}O_2$ was fed to a 20 cm length of blade, with the lower edge of the chamber 30 cm above the cut base, for 5 minutes at 2000 ft-c. The light series received 2000 ft-c by day but were dark at night and their total translocation time was 22 hours. The dark series were in total darkness for a translocation period of 24 hours. All blades upright.

Part	% of relative total counts					
	2000 ft-c		Darkness			
	Cut base in water	sucrose	water		sucrose	
	Blade 1	2	3	4	5	6
Apex	3.2	2.9	14.3	33.1	25.7	42.2
Fed part	67.8	70.4	83.7	65.8	74.1	57.2
Base	28.9	26.7	2.0	1.1	0.1	0.6
RTC × 10^6	5.8	6.9	5.0	3.6	5.0	4.4

and since darkening the apex or the base changes the percentage of translocation to these parts presumably by creating sinks due to changes in gradients of sugar (due to lack of photosynthesis in the darkened area), the attempt was made to change the sugar gradient by the absorption of sugar through the cut base or apex.

Sucrose absorbed by a cut base did not change the direction of translocation in the light or in darkness (table X). Sucrose absorbed by a cut apex, at 2000 ft-c, inhibited the small apical translocation but did not increase basal translocation (fig 15). In darkness, sucrose absorbed by a cut apex decreased apical translocation and increased basipetal translocation (fig 15). This effect was due to sugar, not osmotic concentration, since neither NaCl nor mannitol of osmotic pressure equivalent to the sucrose solution had any effect (table XI).

The effect was not confined to sucrose, but was obtained with several other sugars: maltose, glucose, mannose, and xylose (table XII). Maltose and glucose, of course, can be converted to sucrose within the cane blade, but mannose cannot. How mannose and xylose act has not been determined. Even malic acid appeared to have a slight effect. Whatever the kind, the absorbed sugar is presumed to move primarily up the xylem, but enough found its way into the phloem to drive the C^{14}-sucrose toward the base.

The gradient of sugar is thus a primary factor governing the direction and percentage of translocation, both in the dark and in the light. But it is not the only requirement. An unknown factor enables an afternoon blade to continue translocation in the dark after the accumulation of sugar in the basal parts has reversed the sucrose gradient, and enables a morning blade to do so in the light. Continued photosynthetic production of sucrose might be the essential requirement for morning blades, but not for afternoon blades in the dark. Afternoon blades must already contain the essential factor which morning blades make in the light.

Effect of 3-(parachlorophenyl)-1, 1-dimethylurea

Table XI

Effect of Standing Cut Apex in Water, Sucrose, Mannitol, or NaCl upon Translocation for 24 Hours by AM Blades in the Dark

Detached blades with the cut base standing in tap water were preilluminated at 2000 ft-c and then fed 10 μc of $C^{14}O_2$ for 5 minutes at 2000 ft-c, with the lower edge of the feeding chamber placed 30 cm above the cut base. After feeding, the apex was cut off (under water) 30 cm above the fed part, and the cut apex stood in water or solutions and placed in total darkness. Final composition of solutions, all prepared with tap water: Sucrose, 2.5 % (73 mM); mannitol, 1.33 % (73.1 mM); NaCl, 0.214 % (36.7 mM). All blades upside down in the dark.

Part	% of relative total counts							
	Water		Sucrose		Mannitol		NaCl	
	Blade 1	5	2	6	3	7	4	8
Apex	17.1	13.0	0.5	0.3	9.9	17.7	26.1	17.5
Fed	65.9	80.3	79.9	61.6	83.4	77.3	67.5	66.5
Base	16.9	6.7	19.6	38.1	6.7	5.0	6.3	16.0
RTC × 10^6	4.8	4.0	2.7	4.1	3.6	3.7	4.1	4.1

Table XII

Effect of Standing Cut Apex in Sugars or Malic Acid upon Translocation for 24 Hours by AM *Blades in the Dark*

The method of feeding and handling the blades was the same as in table XI. Final composition of solutions, all prepared with tap water: sucrose, 2.5 % (73 mM); maltose, 2.6 % (73.1 mM); glucose, 1.25 % (69.4 mM); mannose, 1.3 % (72 mM); xylose, 1.1 % (72.4 mM); malic acid, 0.5 % (37 mM), not neutralized (pH 2.6). All blades upside down in the dark.

Cut apex standing in	% of relative total counts			RTC × 10^6
	Apex	Fed part	Base	
Tap water	18.8	75.8	5.3	6.7
Tap water	22.9	73.7	3.5	4.8
Sucrose	0.4	62.5	37.1	4.7
Sucrose	2.3	84.7	12.9	4.4
Maltose	0.6	69.1	30.3	4.5
Maltose	0.4	78.5	21.1	5.0
D-Glucose	2.6	82.1	15.3	4.5
D-Glucose	6.7	77.1	16.2	4.6
D-Mannose	2.8	74.9	22.3	4.1
D-Mannose	5.8	79.0	15.2	4.3
D-Xylose	3.8	73.9	22.2	5.9
D-Xylose	3.0	82.4	14.5	4.1
L-Malic acid	3.2	91.6	5.2	4.9
L-Malic acid	6.3	86.0	7.7	4.1

(CMU). An experiment was conducted to determine if the photophosphorylative production of ATP might be the factor required to drive the translocation

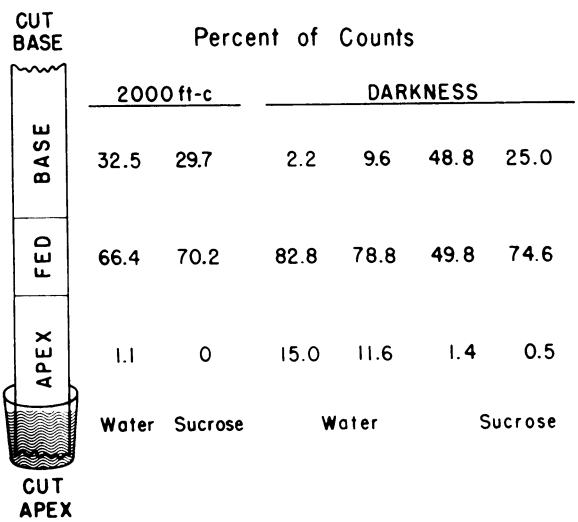

FIG. 15. Effect of absorption of sucrose by the cut apex of morning blades upon translocation at 2000 ft-c and in the dark. $C^{14}O_2$ (10 μc) was fed to a 20-cm length of blade for 5 minutes at 2000 ft-c, at a position 30 cm above the cut base. After feeding, the apex was cut off (under water) and the cut apex stood in water or 2.5 % sucrose (72 mM) for translocation. Left, translocation for 22 hours (2000 ft-c by day, dark from 4 PM to 8 AM). Right, translocation for 24 hours in the dark room. Relative total counts × 10^6: light, in water, 7.6; light, in sucrose, 7.4. Darkness, in water, 3.3, 4.2; darkness, in sucrose, 4.6, 4.4. All the blades were upside down.

Table XIII

Effect of CMU on Translocation

Detached blades standing in tap water were fed 10 μc of $C^{14}O_2$ for 5 minutes at 2000 ft-c with the lower edge of the chamber 50 cm above the cut base. After removing the chamber, the fed part was dipped for an instant into a solution of CMU. The blades were then allowed to translocate for 2 hours at 2000 ft-c. Dripping down of the CMU below the fed part was prevented by wiping with cotton. Concentration of CMU: 120 mg per liter of 0.5 % turgitol (0.606 mM).

Part	% of relative total counts			
	Control		Dipped in CMU	
	Blade 2	4	1	3
Apex	0.3	0.2	0.3	0.2
Fed	62.2	64.8	81.6	86.1
Base	37.5	35.1	18.2	13.6
RTC × 10^6	9.0	7.6	7.6	8.0

of sucrose down the blade, as suggested by the results of Kendall (15) using P^{32}. Kursanov (16, 17) reported that enriching beet leaves with ATP accelerated the movement of assimilates from the mesophyll into the conducting cells and movement toward the roots. If ATP is a requirement for the translocation of sucrose in sugarcane blades, that might explain the inhibitory effect of high intensities of light (e.g. 8,000 ft-c) mentioned in Methods, since Avron (2) reported that adenosine triphosphatase of Swiss chard chloroplasts is active at 130,000 lux.

The effect of CMU was studied, since CMU is said to inhibit the formation of ATP (14). After removing the feeding chamber, the fed part of the blade was dipped instantaneously into a solution of CMU (120 mg CMU/liter of 0.5 % turgitol or 0.606 mM). The blade was then placed in normal position for translocation at 2000 ft-c. This treatment decreased the percentage of basipetal translocation (table XIII). Supplying ATP to the cut end had no beneficial effect on translocation, but there is doubt as to whether any was absorbed.

Gradient in Moisture Percentage. The finding that mannose and xylose, which are not converted to sucrose, as well as glucose and maltose are able to reverse the direction of translocation by morning blades in the dark (table XII) favors the mass flow theory rather than the diffusion theory. Mass flow requires a difference in hydrostatic pressure, greater at the source than at the sink (29). For mass flow to cause translocation in detached blades, the apex should have a higher percentage of moisture than the base. However, sugarcane blades cut from the plant in either the morning or the afternoon, and analyzed for moisture with no previous experimentation, have much lower percentages of moisture at the apex than at the base (table XIV). Different tissues will, of course, have different percentages of moisture, but it seems reasonable to assume that if one tissue has more water, other adjacent tissues also have more water.

Table XIV

Moisture Gradient in Blades

Moisture percentages in blades showing negative gradients from apex to base.

cm above cut base	Time cut			
	8:07	8:17	2:30	2:43
100 and above	...	68.6	65.4	64.3
80–100	68.2	71.0	68.9	66.8
60–80	71.2	73.1	71.3	69.3
40–60	73.3	75.9	73.3	72.9
20–40	76.6	77.7	74.7	76.1
0–20	80.2	81.2	78.3	79.9

If so, the moisture gradient in the leaf is the reverse of that required by the pressure flow hypothesis.

Discussion

Before considering the bearing of these results on the theories of the mechanism of translocation, one must ask whether conclusions based on experiments with detached blades are applicable to the translocation process in entire plants. Schumacher and Hülsbruch (24) warned that conclusions about the mechanism of translocation in intact plants are not necessarily valid when drawn from results with severed parts. Workers successfully using detached leaves for studies of translocation include Leonard (18) and Thaine et al (26). Many workers use severed parts for studying the transport of auxin. In sugarcane, the following results from studies with the entire plant are the same as those obtained with detached blades: translocation in the blade is polar, being almost entirely basipetal (12); polarity is not affected by gravity (Annual Report, 1961; Experiment Station, HSPA, p 11); translocation is not affected by transpiration (11); actively growing lateral and basal shoots acting as sinks increase the percentage of translocation downwards (11); darkening the fed blade decreases translocation from it (11).

Since many of the data available are similar for detached and attached blades, we are of the opinion that conclusions drawn from studies with detached blades are applicable to the translocation process in entire plants of sugarcane.

Polarity. Polarity of translocation of photosynthate involves 2 aspects: the polar transfer of sucrose from mesophyll cells to phloem, and the polar transport of sucrose within the phloem. Experiments reported here deal with the second aspect. C^{14} sucrose made in the fed part was translocated primarily basipetally in the light, regardless of the position of the blade. Acropetal translocation in the dark was also independent of orientation of the blade. Thus a means has been found to study polar transport experimentally. No such means had previously been found (3) although the polar transport of sugar was demonstrated in beet leaves (18) and of auxin in coleoptiles (31, 32). Polarity in plants was reviewed by Bloch (5).

The importance of establishing the existence of polarity in the transport of sucrose in the phloem was recognized by Mason, Maskell, and Phillis (19) who stated that if phloem transport were polar, the observed high rates of solute movement might be attained by the polar concentration of sucrose across each sieve plate from source to sink.

Crafts (6) stated that no one has yet demonstrated polar movement longitudinally in sieve tubes. Weatherley, Peel, and Hill (30) using isolated stem segments and irrigated strips of bark, found no polarity of movement. Zimmermann (34) stated that as far as known, sieve tubes as such do not exhibit polarity of transport. Yet the major percentage of translocation in an attached leaf is basipetal (12, 26, 27). Zimmermann (35) tried to find an effect of gravity in trees detached from their roots, and found no effect. Hartt inverted an entire plant of sugarcane and found the same percentage distribution of C^{14} as in an upright plant.

While experiments with entire plants ruling out gravity as a factor may suggest the existence of polarity in transport, a definite separation of polarity from pulling forces exerted by the remainder of the plant is not possible. In the experiments reported herein, these pulling forces of the rest of the plant were, of course, eliminated by detachment of the blade from the sheath. Since basipetal translocation in the light was always found regardless of orientation of the blade, definite evidence of a strong basipetal polarity in translocation of sucrose is proved for sugarcane blades. A similar polarity is not found in the stem as a whole, since upward and downward translocation of C^{14} occur simultaneously, although not necessarily in the same sieve tubes (12). The basipetal polarity of sucrose transport in the leaf constitutes an important part of the mechanism whereby the leaf exports its sugar into the stem. This polarity of sucrose transport in the leaf may be the specific factor from leaves needed for the proper functioning of phloem mentioned by Zimmermann (34).

The reversal of polarity in leaves depending upon growth and development has been mentioned for other plants (18, 25, 26). The reversal of polarity in a detached blade in total darkness is an immediate effect. It is not a destruction of polarity, as is the effect of triiodobenzoic acid on auxin (21), but rather is the reversal of polarity. Since this reversal cannot be due to initial sucrose gradients (they being the same), nor to a sink when the entire leaf is dark, there must be some other explanation. This immediate response must be due to an immediate change in the darkened leaf. One of the most immediate changes in protoplasm upon darkening is in viscosity. Virgin (28) stated that viscosity increases rapidly in darkness. Permeability and other factors change along with viscosity. Surface tension increases when viscosity increases (33). Changes in the physicochemical properties of protoplasm may play a role in the reversal of polarity by darkness.

Polar transport is not dependent upon the substance moving, because it is shown for such diverse

compounds as sucrose and auxin. Neither is polar transport dependent upon the tissue used, because it has been demonstrated for auxin in both xylem and phloem (23) in twigs, meristem in peanut gynophore (13) and elsewhere. Since in sugarcane polar transport is apparently dependent upon light or a light-formed factor, polar transport may be related to the physicochemical properties of protoplasm and/or a supply of energy.

Sugar Gradients. The importance of sugar gradients in entire plants in determining direction and rate of translocation was emphasized by Mason and Phillis (20). The present study illustrates the importance of natural or artificial gradients in determining translocation in a detached blade of sugarcane, in which a positive gradient enables translocation to take place in the dark, and the absence of a gradient prevents translocation in the dark. But during translocation by blades in the light, and by blades with an initial positive gradient in the dark, sucrose moves down the blade to the cut base and accumulates. This accumulation is in the veins, not in the parenchyma, being conspicuous in the lower midrib. Light, or a light-formed factor, pushes the sucrose in a basipetal direction even against the gradient, once translocation has started.

Movement to and from Darkened Areas. Our results have shown definitely that sucrose moves from the fed part into darkened areas of the detached blade. We have called this an example of movement from source to sink, the darkened area (which may be either the apex or the base) constituting a sink because of the cessation of photosynthesis. Other possible explanations include the immediate change in viscosity of protoplasm following darkening (28), which may result in increased surface tension and changes in other physicochemical properties of protoplasm. The solvent capacities of the tissues may differ in light and dark; Mason and Phillis (20) recognized the importance of differences in solvent capacities for sucrose which may be characteristic of various tissues. Changes in permeability of the sieve tubes following darkening may explain translocation to darkened areas, since (a) viscosity increases immediately upon darkening (28), (b) permeability is affected by viscosity (28), and (c) sieve tube semipermeability was shown by Zimmermann (34) to be a reversible process, enzymic, with the direction possibly controlled by a leaf stimulus.

With attached leaves there is little if any movement into darkened leaves or parts of leaves (1). Thaine et al. (26) found no movement of C^{14} into shaded upper halves of attached leaves, but definite movement into masked apical halves of detached leaves. It may be that in an attached leaf the pull from below is enough to overcome the pull from the darkened area of the leaf. Darkening an attached leaf of sugarcane decreased its ability to translocate C^{14} sucrose to the stem (11) which was considered evidence of competing streams.

Bearing of Results on Theories of Translocation. The results presented herein have a bearing on 2 of the chief theories of the mechanism of translocation, viz. the diffusion theory and the mass flow theory. The fact that sucrose can go against the gradient while moving in the veins and can accumulate in the base of the blade (tables 1, 8) particularly in the midrib (fig 2), is against the diffusion theory. Also, if diffusion were the mechanism, even activated diffusion, only more sucrose coming in the cut apex could reverse the polarity of translocation in the dark. Our studies have shown that the direction of translocation in the dark can be reversed not only by sucrose and sucrose-forming sugars (glucose and maltose) but by other sugars (mannose and xylose). This effect of mannose and xylose could well be explained by the conventional mass flow hypothesis, which requires that different kinds of molecules move together in a stream. Swanson (25) emphasized that in mass flow it is the difference in total concentration of solutes between source and sink which causes the turgor-pressure gradient needed to drive the flow. Translocation in an entire plant certainly resembles a stream, with competing streams coming down from each leaf (11). Mass flow requires a permanent supply of sucrose or other solute at the source; a good illustration is our all-night leaf punch test in which translocation stopped when the sucrose counts nearly ran out and started again following the conversion of residue counts to sucrose counts (10).

But mass flow requires a sink and detached blades exhibit translocation without a sink, even at times against the gradient of sucrose. Mass flow also requires a difference in hydrostatic pressure, the stream of solvent plus solute moving from a region of high pressure to a region of low pressure. But in detached blades, sugar goes from a place of low moisture percentage to a place of high moisture percentage. True, these moisture percentages are of the entire blade section; but if one tissue has more water, it may be assumed that other adjacent tissues also have more water.

Swanson also states that the difference in turgor pressure causing mass flow can be obtained against the total concentration gradient if the walls at the source are more extensible than the walls at the sink. But in sugarcane, sugar entering from a young blade, such as blade 4 or 5, moves down the stem from a young joint with more extensible walls to older joints with less extensible walls, which is the reverse condition from that mentioned by Swanson.

Since neither the water gradient nor the ultimate sucrose gradient in detached blades is that required by the conventional theory of mass flow, if it is a mass flow, it must be an activated mass flow—the driving force coming from something other than differences in turgor pressure.

The authors have recently proposed (11) that translocation in the sieve tube of the stem requires the enzyme systems identified by Glasziou and coworkers (7) and by Bieleski (4) as functioning in transfer from sieve tube to parenchyma in storage internodes of sugarcane. A similar system of sugar transformations functions in the blade (8) and should

be considered in any theory of the mechanism of polar transport in the sieve tube of the blade.

The results presented in this report demonstrate a strong effect of light upon polarity and translocation of sugar in detached blades. Therefore, experiments on the effects of light intensity and quality upon translocation in severed blades have been undertaken in an attempt to elucidate the mechanism by which light affects translocation in sugarcane (10).

Summary

Translocation of C^{14}-photosynthate takes place in detached blades of sugarcane, following the veins to the midrib and accumulating at the base of the blade.

The velocity of translocation in detached blades is 0.4 centimeters per minute; this is slower than in attached blades where the velocity ranges from 0.7 to over 2 centimeters per minute.

Sucrose is the principal compound moving.

Cutting off the apex just above the fed part has no effect on translocation.

At 2000 foot-candles major transport is basipetal, and this polarity is not changed by standing a blade upside down.

P^{32} as orthophosphate is absorbed by a detached blade and moves upward regardless of which end of the blade is standing in P^{32} solution.

The translocation of C^{14}-photosynthate does not require a sink but the amount translocated is greatly increased by supplying a sink.

Darkening the base or apex of the blade increases the amount of translocation thereto.

Darkening the fed part curtails translocation to the base; darkening the fed part plus cutting off the apex almost completely inhibits translocation.

Darkening the entire blade (cut in the early morning) generally reverses the polarity of translocation, causing more counts to go to the apex than to the base; and this polarity of dark translocation to the apex is unaffected by the pull of transpiration, gravity, or position of the blade for which reason apical translocation in the dark is considered to take place in the phloem.

The decrease in basipetal translocation in the dark, in blades cut in the morning, is not prevented by supplying additional sucrose to the cut base of the blade, and is therefore not a starvation phenomenon.

Basipetal translocation in the dark depends on the time of day the blade is cut, being small in morning blades and increasing during the day. Blades cut in the middle of the afternoon can translocate very well in total darkness.

Blades cut in the morning differ very little in percentage of sucrose along their length, whereas blades cut in the afternoon have a strong positive gradient in sucrose (2 or more times higher in the apex than in the base); thus basipetal translocation in the dark is initiated only in blades with a positive gradient in sucrose.

As translocation proceeds, sugar accumulates in the basal sections and the final sucrose gradient is the reverse of the initial.

The absorption of sucrose by the cut apex of a morning blade reverses the polarity of translocation in the dark. No such effect was obtained with mannitol or NaCl in the same osmotic concentration as the sucrose.

Other sugars with effects similar to sucrose include maltose, glucose, mannose, and xylose.

Since afternoon blades in the dark, as well as morning blades in the light, can continue translocation against the gradient in sucrose, there must be a regulating factor other than continued photosynthesis of sucrose.

Since dipping the fed part into 3-(parachlorophenyl)-1, 1-dimethylurea, which inhibits the formation of adenosine triphosphate, considerably decreased basipetal translocation, adenosine triphosphate may be required to drive the translocation of sucrose against the gradient.

The translocation of photosynthate in sugarcane depends upon the strong basipetal polarity within the phloem of the blade, and is primarily a push from the leaf, the push being dependent upon light, upon the gradient in sugar, and possibly upon a regulating factor.

Acknowledgments

Grateful appreciation is expressed to Miss Ada Forbes and Mrs. Grace Sadaoka for technical assistance.

Literature Cited

1. Aronoff, S. 1955. Translocation from soybean leaves. II. Plant Physiol. 30: 184–85.
2. Avron, M. 1962. Light dependent adenosine triphosphatase in chloroplasts. J. Biol. Chem. 237: 2011–17.
3. Biddulph, O. 1959. Translocation of inorganic solutes. In: Plant Physiology, a Treatise. F. C. Steward, ed. 2: 553–603.
4. Bieleski, R. L. 1962. The physiology of sugarcane. V. Kinetics of sugar accumulation. Australian J. Biol. Sci. 15: 429–44.
5. Bloch, R. 1943. Polarity in plants. Botan. Rev. 9: 261–310.
6. Crafts, A. S. 1951. Movement of assimilates, viruses, growth regulators, and chemical indicators in plants. Botan. Rev. 17: 203–84.
7. Glasziou, K. T., M. D. Hatch, and J. A. Sacher. 1963. Accumulation and transformation of sugars in sugar cane storage tissue. Proc. Intern. Soc. Sugarcane Technologists, 11th Congr. 1962: 334–38.
8. Hartt, C. E. 1943. The synthesis of sucrose in the sugar cane plant. I, II, III. Hawaiian Planters' Record 47: 113–132, 155–170, 223–255; 1944. IV. 48: 31–42.
9. Hartt, C. E. 1962. Translocation of C^{14} in detached blades of sugarcane. Plant Physiol. 37: xii.
10. Hartt, C. E. 1964. Translocation of sugar in the cane plant. 1963 Reports, Hawaiian Sugar Technologists, 22nd Annual Meeting, p 151–67.
11. Hartt, C. E., H. P. Kortschak, and G. O. Burr. 1964. The effects of defoliation, deradication, and darkening the blade upon translocation of C^{14} in sugarcane plants. Plant Physiol. 39: 15–22.

12. HARTT, C. E., H. P. KORTSCHAK, A. J. FORBES, AND G. O. BURR. 1963. Translocation of C^{14} in the sugarcane plant. Plant Physiol. 38: 305–18.
13. JACOBS, W. P. 1951. Auxin relationships in an intercalary meristem: further studies on the gynophore of *Arachnis hypogaea* L. Am. J. Botany 38: 307–10.
14. JAGENDORF, A. T. AND M. MARGULIES. 1960. Inhibition of spinach chloroplast photosynthetic reactions by *p*-chlorophenyl-1, 1-dimethylurea. Arch. Biochem. Biophys. 90: 184–95.
15. KENDALL, W. A. 1955. Effect of certain metabolic inhibitors on translocation of P^{32} in bean plants. Plant Physiol. 30: 347–50.
16. KURSANOV, A. L. 1961. The transport of organic substances in plants. Endeavour 20: 19–25.
17. KURSANOV, A. L. AND M. I. BROVCHENKO. 1961. Effect of ATP on the entry of assimilates into the conducting system of sugar beets. Fiziol. Rast. (Eng. trans.) 8: 211–17.
18. LEONARD, O. A. 1939. Translocation of carbohydrates in the sugar beet. Plant Physiol. 14: 55–74.
19. MASON, T. G., E. J. MASKELL, AND E. PHILLIS. 1936. Further studies on transport in the cotton plant. III. Concerning the independence of solute movement in the phloem. Ann. Botany (London) 50: 23–58.
20. MASON, T. G. AND E. PHILLIS. 1937. The migration of solutes. Botan. Rev. 3: 47-71.
21. NIEDERGANG-KAMIEN, E. AND F. SKOOG. 1956. Studies on polarity and auxin transport in plants. I. Modification of polarity and auxin transport by triiodobenzoic acid. Physiol. Plantarum 9: 60–73.
22. NISHIDA, K. 1962. Studies on the reassimilation of respiratory CO_2 in illuminated leaves. Plant and Cell Physiol. 3: 111–24.
23. OSERKOWSKY, J. 1942. Polar and apolar transport of auxin in woody stems. Am. J. Botany 29: 858–66.
24. SCHUMACHER, W. AND M. HÜLBRUCH. 1955. Zur Frage der Bewegung Fluorescierender Farbstoffe im Pflanzenkörper. Planta 45: 118–24.
25. SWANSON, C. A. 1959. Translocation of organic solutes. In: Plant Physiology, a Treatise. F. C. Steward, ed. 2: 481–551.
26. THAINE, R., S. L. OVENDEN, AND J. S. TURNER. 1959. Translocation of labelled assimilates in the soybean. Australian J. Biol. Sci. 12: 349–72.
27. VERNON, L. P. AND S. ARONOFF. 1952. Metabolism of soybean leaves. IV. Translocation from soybean leaves. Arch. Biochem. Biophys. 36: 383–98.
28. VIRGIN, H. I. 1961. Plant cell response to visible light excluding photosynthesis. In: Progress in Photobiology. B. C. Christensen and B. Buchmann, eds. Elsevier Publishing Co., New York. p 15–26.
29. WEATHERLEY, P. E. 1962. The mechanism of sieve tube translocation: observation, experiment, and theory. Advan. of Sci. 18: 571–77.
30. WEATHERLEY, P. E., A. J. PEEL, AND G. P. HILL. 1959. The physiology of the sieve tube. Preliminary experiments using aphid mouth parts. J. Exptl. Botany 10: 1–6.
31. WENT, F. W. 1928. Wuchsstoff und Wachstum. Rec. Trav. Botan. Néerl. 25: 1–116.
32. WENT, F. W. AND K. V. THIMANN. 1937. Phytohormones. The MacMillan Co., New York. 294 pp.
33. YOUNG, C. B. F. AND K. W. COONS. 1945. Surface active agents. Chemical Publishing Co., Inc., Brooklyn, New York. 381 pp.
34. ZIMMERMANN, M. H. 1960. Transport in the phloem. Ann. Rev. Plant Physiol. 11: 167–90.
35. ZIMMERMANN, M. H. 1962. Translocation of organic substances in trees. V. Experimental double interruption of phloem in white ash (*Fraxinus americana* L.). Plant Physiol. 37: 527–30.