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Translocation of Assimilates and Phosphate in Detached Bean Leaves

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Abstract. ^{14}C-assimilates were accumulated by the veins in the blades and transported basipetally into the petioles of detached leaves of Red Kidney bean (*Phaseolus vulgaris* L.). Neither process was greatly affected by mild moisture stress, age of fully enlarged leaves, or period in the dark prior to exposure to $^{14}CO_2$. However, both vein loading and transport into petioles were greatly reduced by oxygen deficiency. The basipetal transport of $^{32}PO_4$ also did not appear to be greatly reduced by 6 or 8 days of darkness prior to the application of phosphate-^{32}P, followed by a transport period of 1 day in the dark. Endothall at 5×10^{-3} M was effective in stopping basipetal flow of ^{32}P. It is considered that transport in leaves may be powered by forces in the plasmodesmata of the cell walls between the border parenchyma and phloem.

Twenty-nine years ago the senior author (12) observed that sugars were translocated in detached sugar beet leaves from the laminae into the petioles. The sugars accumulated rather uniformly in different parts of the petioles, with no indication of any special accumulation in the basal section. It was suggested that the basipetal flow in the petioles was due to a polarity originating in the border parenchyma of the veins of the blades. Barrier and Loomis (1) later described vein loading in detached leaves using ^{14}C-2,4-D and $^{32}PO_4$. More recently Hartt and Kortschak (6), Nakata and Leopold (18) and Hartt (8) studied polar transport in detached leaves and blades. Hartt's work (8) indicated that polar transport initiation was under photocontrol; however, short exposure of sugarcane blades to light (5 min at 200 ft-c) was not enough to drive basipetal translocation.

Following transport of labeled translocate for several hours, labeling of veins and petioles is greater in detached leaves than in leaves attached to plants. This makes them suitable for studying factors affecting transport. Further, the leaf is a simple system when compared with a whole plant, and can be separated into the blade as the source and the petiole as the sink. Due to this simplification, we could explore the effects of several factors on vein loading and transport including leaf age, light, period of predarkening, period of detachment, oxygen supply, *etc.*

Materials and Methods

Seeds of Red Kidney bean (*Phaseolus vulgaris* L.) were planted in 4-inch pots and later thinned to 1 plant per pot. When the primary leaves were well expanded they were exposed in a polyethylene or plexiglass chamber in sunlight to 50 μc $^{14}CO_2$. The petioles were wrapped with aluminum foil to prevent photosynthetic incorporation of $^{14}CO_2$ by the petioles. In some tests, the detached leaves or whole plants were subjected to various dark periods before being exposed to $^{14}CO_2$. When whole plants were used, the leaves were detached immediately following the exposure. Some leaves were freeze-dried directly following their exposure to $^{14}CO_2$, while others were placed in moist chambers for varying periods to allow transport to go on. In most instances, transport occurred while the leaves were in the dark, with the petioles either in water or in air.

In other tests, 5 to 25 μc of phosphoric acid-^{32}P neutralized with NH_4OH was applied per leaf in 5 μl of water. The applications were made in the laboratory with the overhead lights turned off and the leaves returned to the dark moist chambers within a few minutes following treatment. Other aspects of experimentation were the same as for $^{14}CO_2$.

Some experimental details will be described along with the results since several types of experiments were conducted.

Specific activity measurement, chromatography, and autoradiography were conducted by methods described by Hull and Leonard (9) and Crafts and Yamaguchi (4). In all instances the leaves were freeze-dried before being autoradiographed.

Results

Transport of ^{14}C-Assimilates Into Petioles After Various Periods of Time. Directly following exposure to $^{14}CO_2$, labeled assimilates were found in those parts of the blade containing chloroplasts, with

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the veins and petioles having only traces of label in them (14). Within 30 minutes, labeled assimilates were clearly accumulating in both the veins in the blades and in all parts of the petioles, with the greatest labeling being in the upper part of the petioles. Labeled assimilates continued to move from the blades into the petioles for 480 minutes, with the greatest movement occurring during the first 120 minutes (table I). There was no evidence of any special accumulation of labeled assimilates in any segment of the petiole. Thus the pattern of distribution after a few hours was one of fairly uniform distribution from top to base.

Narrow strands within the leaf veins were lightly labeled in 30 minutes. Labeling increased with time and then decreased in the smaller veins; however, labeling of the major veins and midrib continued to increase for the duration of the test (18 hrs).

Autoradiography of cross sections (20–30 microns thick) of petioles revealed that most label was concentrated in the veins. Longitudinal sections of the basal part of the petioles did not show any special accumulation.

Chromatography of 80 % ethanol extracts of the blades and different sections of the petioles revealed that 86 % of the labeled sugars in the blades was in the form of ^{14}C-sucrose 6 minutes after the leaves were placed in an atmosphere containing $^{14}CO_2$, while no detectable labeled sugar was in the petioles. After 24 hours, only about 20 % of the labeled sugar in the blades was sucrose, with the remainder being 50 % glucose, and 30 % fructose. At this time, the upper part of the petiole contained about 50 % sucrose, 34 % glucose, and 16 % fructose, while the lower part contained 66 % sucrose, 22 % glucose, and 12 % fructose. Sucrose, which is considered as being the main assimilate transported, was evidently partially inverted after moving out of the transport channels in the veins of the blades and petioles.

The water bathing the bases of the petioles always contained appreciable label. To investigate the nature of this label and when it was lost from the petioles, 20 leaves were exposed to $^{14}CO_2$ and then placed in moist chambers with the petiole bases in water. Total leakage was 1413 cpm from 0 to 6 hours, 148 cpm from 6 to 12 hours, and 698 cpm from 12 to 24 hours. The leachate, when concentrated and chromatographed, was found to have most of the label in sucrose, with none evident in either glucose or fructose.

Effect of Predarkening on Transport. Bean plants, kept in the dark for 0 to 7 days, were exposed to $^{14}CO_2$ from 1 to 10 minutes. The leaves were then detached and placed in the dark in moist sandwich boxes, with petiole bases in water, for 24 hours. The leaves were freeze-dried, autographed, and subsequently counted. Only the counting data are shown (table II).

Vein loading and transport of ^{14}C-assimilates from blades into the petioles occurred irrespective of period of predarkening or whether the leaves were exposed to $^{14}CO_2$ for 1 or 10 minutes. Only the data following 1-minute exposure are shown (table II). The results obtained with the 10-minute exposure were similar, except that the carbon fixed in the blades and transported into the petioles was 5 to 10 times greater. Not only did labeled assimilates migrate into the petioles in plant predarkened for 7 days, but the distribution of label within the petiole was uniform from top to base.

The effect of 0 to 6 days predarkening on the transport of labeled assimilates in whole bean plants was determined. The plants were exposed to $^{14}CO_2$ for 5 minutes and then returned to the dark for 24

Table I. *Distribution of ^{14}C Between Blades and Petioles of Detached Leaves at Different Intervals Following Their Exposure to $^{14}CO_2$ for 10 Minutes*

The leaves were detached immediately following exposure of the plants to $^{14}CO_2$.

Leaf part	Transport period in min						
	10	30	60	120	240	480	1080
	cpm/leaf part						
Blade	15000	15000	14000	13000	13000	11000	12000
Petiole	30	299	1087	2225	2329	2769	2415

Table II. *Effect of Length of Prior Dark Period on Radioactivity in Blades and Petioles of Detached Leaves Immediately and 24 Hours After Their Exposure to $^{14}CO_2$ for 1 Minute in Sunlight*

The leaves were detached immediately following exposure and either freeze-dried or stored in a dark moist chamber for 24 hours.

Leaf part	Days stored in dark									
	Transport period									
	1 min	24 hr	1 min	24 hr	1 min	24 hr	1 min	24 hr	1 min	24 hr
	cpm/leaf part $\times 10^{-1}$									
Blade	2000	1600	750	500	420	260	75	35	45	35
Petiole	2.2	310	0.6	185	0.6	120	0.4	4	0.5	1.6

Table III. *Effect of Various Periods of Predarkening on the Transport of $^{32}PO_4$ From Blades Into the Petioles of Attached and Detached Leaves*

The leaves or plants were stored in a dark moist chamber for 24 hours following application of the $^{32}PO_4$. One-half of the detached leaves had the bases of the petioles in water.

Days of predarkening	Leaves attached	Leaves detached: Petioles in air	Leaves detached: Petiole bases in water
	cpm/petiole × 10^{-2}		
0	31	200	500
2	36	240	700
4	23	120	300
6	23	120	120

hours, freeze-dried and autographed. The presence of label in the roots was shown by the autoradiographs, indicating that labeled assimilates had been moved into them, even after 6 days of predarkening.

In another test, leaves were detached from bean plants that had been in the dark for 0, 2, 4, and 6 days. Directly following detachment, 5 μl of water containing $^{32}PO_4$ were applied to the major veins of the blades; the bases of the petioles were in air or in water in dark moist chambers for 24 hours. In simultaneous tests, $^{32}PO_4$ was applied to leaves attached to plants, with the dark periods being the same as with detached leaves.

Results from counting and autoradiography (table III) agree except in detail. ^{32}P migrated from the blades into the petioles with all periods of predarkening. The data suggest that there was some drop-off in total activity in petioles after 2 days of predarkening. More label migrated into petioles when the bases were in water than when in air. Petioles contained the least label when they were on leaves attached to plants; some of the label had migrated out of the leaves into the stems and sometimes into the roots. This accounts for the lower quantity of label in the petioles of attached leaves than in petioles of detached leaves.

Detached leaves with petioles in water lost label that leaked into the water. The loss per leaf was 505 cpm for leaves that had not been predarkened, 650 cpm for those predarkened for 2 days, 200 cpm for those predarkened 4 days, and 530 cpm for those predarkened 6 days. Evidently, predarkening did not greatly influence the loss of ^{32}P from the petioles of leaves.

One might criticize this experiment (table III) because the leaves were treated soon after detachment which could have created a sudden, unnatural sink at the base of the petioles by opening the transport channels. In order to minimize this effect, leaves were detached for 5 hours prior to being treated with $^{32}PO_4$. Other aspects of the test were the same as described above, except the predarkening period was 8 days. After a transport period of 24 hours, petioles on leaves from plants that were not predarkened contained 39,000 cpm, while those from plants that had been predarkened 8 days had 23,000 cpm. Transport of ^{32}P into the petioles occurred even though the leaves had been detached for 5 hours before application of the label. In this same test, some leaves attached to plants also were treated with this label; 24 hours after being treated, label was present in the roots of plants that had been predarkened for 8 days.

Transport of ^{14}C-Assimilates and $^{32}PO_4$ in Leaves of Different Ages. Leaves were collected from 10, 17, and 23 day old plants. These leaves were treated with either $^{14}CO_2$ or $^{32}PO_4$ and given a 24-hour transport period, with the bases of the petioles in water. A greater percentage of the labeled assimilates were transported into the petioles of leaves from 10-day old plants than from older plants; however, regardless of age, 16 % or more of the assimilated carbon moved into the petioles (table IV). On the other hand, a far lower percentage of the labeled $^{32}PO_4$ was transported from the blades into the petioles in older leaves. The amount varied from 5 % in leaves of 17-day old plants to 0.5 % in leaves of 23-day old plants suggesting that absorption of the $^{32}PO_4$ may have been more difficult in the older leaves than in the younger ones. No absorption problem existed with labeled assimilates since these were formed within the cells from $^{14}CO_2$. Evidently, the petioles of older leaves maintain their sink properties.

Effect of Detachment for One Day and of Light on ^{14}C-Assimilate Transport. Vein loading and transport appeared similar in leaves detached for 1 day prior to exposure to $^{14}CO_2$ and in leaves detached immediately before such exposure (fig 1). However, the mesophyll of the detached leaves 3 and 4 was darker than in leaves 1 and 2, suggesting some impairment of vein loading resulting from detachment for 1 day. This impairment was not influenced by photosynthesis, since leaves in the light produced similar autoradiographs as those in the dark. This effect must have been due to a build-up in the concentration of assimilates in the veins as a result of vein loading, reducing the ability of the veins to deplete the mesophyll.

Table IV. *Distribution of Radioactivity in Detached Leaves From Bean Plants of Different Ages 24 Hours Following Application*

The labeled substances were ^{14}C-assimilates from $^{14}CO_2$ and $^{32}PO_4$.

Age of plants	Part of leaf	Distribution of radioactivity: ^{14}C-assimilates	Distribution of radioactivity: $^{32}PO_4$
Days		%	%
10	Blade	68	97.5
10	Petiole	32	2.5
17	Blade	84	95.0
17	Petiole	16	5.0
23	Blade	79	99.5
23	Petiole	21	0.5

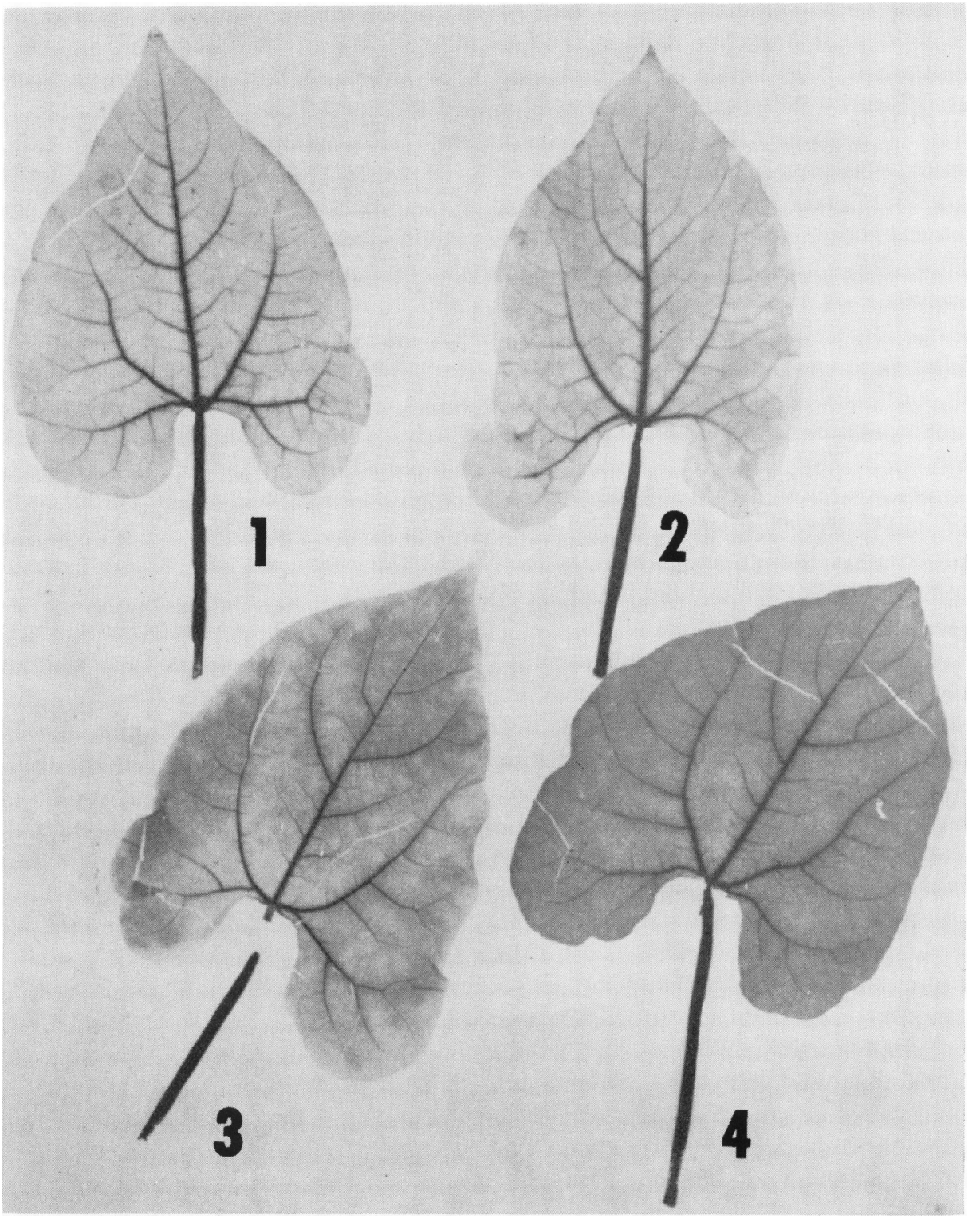

FIG. 1. The effect of detachment and predarkening on the distribution of radioactivity in bean leaves 24 hours after being exposed to $^{14}CO_2$. The leaves were in the dark during the transport period. Only autoradiographs shown. 1) Detached immediately before exposure to $^{14}CO_2$, with prior storage in light. 2) As for No. 1, except prior storage in dark. 3) Detached 1 day prior to exposure to $^{14}CO_2$, with prior storage in light. 4) As for No. 3, except prior storage in dark.

In a test not illustrated, leaves that had been detached for 3 days and stored in the dark prior to exposure to $^{14}CO_2$, did not move appreciable assimilate into the petioles. There was definite accumulation of label at the base of the petioles where callus was forming. Evidently, these newly formed sinks had a marked influence on assimilate distribution within the petioles.

Effects of Darkening and Cutting on ^{14}C-Assimilate Transport. The upper or lower parts of blades attached to plants were covered with aluminum foil for 24 hours or left uncovered. The leaves were then detached and the outer part of the blade trimmed in order to cut many veins. A certain portion of each blade or leaf was exposed to $^{14}CO_2$ for 5 minutes and the leaves were then placed in a dark moist chamber for 24 hours before freeze-drying.

Directly following exposure to $^{14}CO_2$, the label was almost exclusively confined to the exposed area (fig 2). During the transport period of 24 hours, the labeled assimilates were accumulated by the veins and transported mainly in a basipetal direction; however, leaves that had been darkened above the exposed area had label within the veins in this area. Evidently, darkening did induce upward transport, although the main transport was basipetal. There was no evidence that cutting numerous veins in the process of trimming the blades induced transport towards the cut ends.

In some tests with Johnsongrass blades, darkening the upper part did greatly reduce basipetal transport. The results were similar to those obtained by Hartt (8) on sugarcane blades. Evidently differences exist in the transport patterns in leaves of different species; however, vein loading is probably a constant feature with all species.

Crushing the petioles (by rubbing back and forth with a smooth rod) did not stop basipetal flow of labeled assimilates through the crushed parts (fig 2f, h). Evidently, crushing did not destroy the phloem or even injure it sufficiently to block transport. Likewise, crushing usually did not create sinks in the crushed areas—by causing assimilates to leak from the sieve tubes; however, an exception may have occurred in figure 2g (arrow on left).

Cutting the tissue next to the midrib produced a sink within the midrib (fig 2e). This effect may have been due to removal of tissues which normally supply assimilates to the midrib, creating an assimilate deficiency like that produced by shading.

In several tests, leaves were placed in moist chambers following their exposure to $^{14}CO_2$, with the petioles in air or in water (basal 5 mm). After a transport period of 24 hours, the distribution of labeled assimilates was about the same with all treatments. Evidently, an external supply of water was not essential for either vein loading or transport. Autoradiographs are not presented because

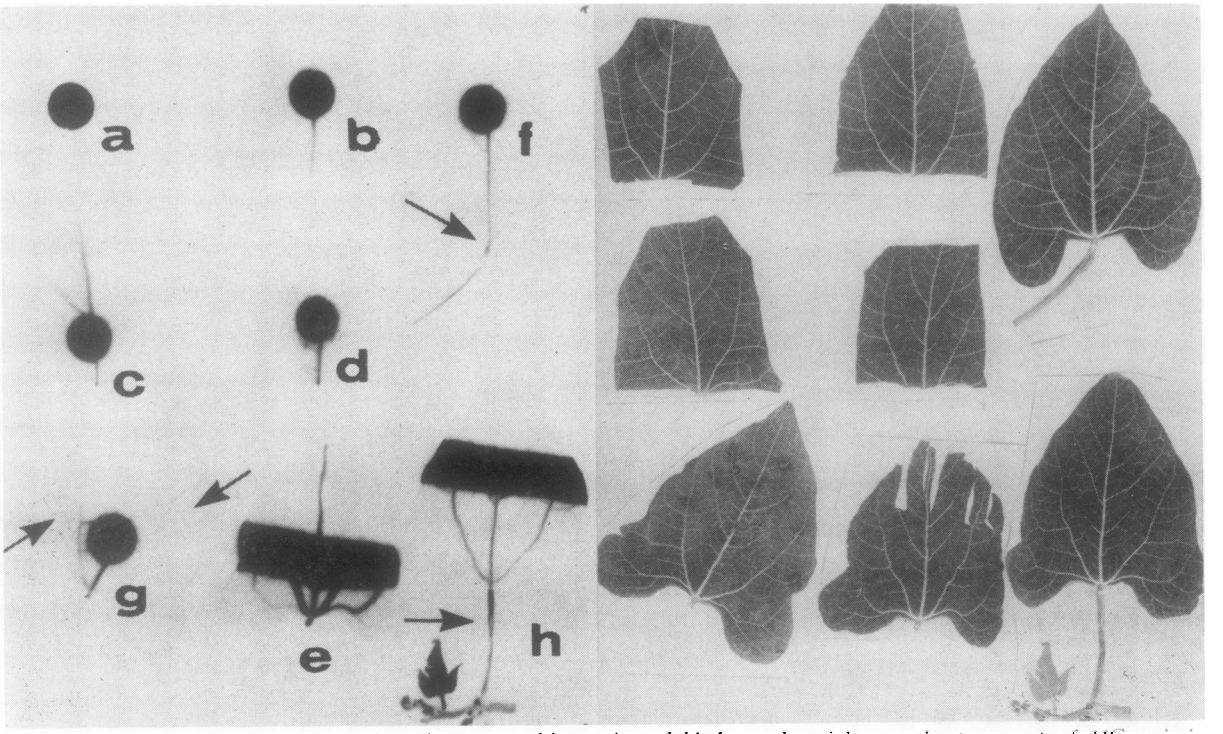

FIG. 2. Effects of darkening and cutting or crushing veins of blades and petioles on the transport of ^{14}C-assimilates out of areas exposed to $^{14}CO_2$. The transport period was 24 hours in the dark. Autoradiographs are on the left (letters apply to these) and mounted leaf parts on the right. a) Blade, directly following exposure, b) no dark pretreatment, c) predarkened above, d) predarkened below, e) veins cut on either side of the midrib, f, g, and h) veins or petioles crushed at points indicated by arrows.

they would essentially duplicate figures already presented.

In other tests, leaves were allowed to air-dry on top of a greenhouse bench following exposure to $^{14}CO_2$. Autoradiographs of these leaves showed that both vein loading and transport into the petioles had occurred in the drying process. Total transport may have been slightly less than in leaves stored in a humid environment.

Oxygen Requirement for Vein Loading and Transport. Leaves were exposed to $^{14}CO_2$ for 5 minutes to form labeled assimilates in the blades. The leaves were then placed in air or in nitrogen gas, with the bases of the petioles in water, or the entire leaves were submerged in water for 6 hours. Transport was in the dark, to prevent photosynthetic oxygen from becoming available to the leaves.

Both vein loading and transport into the petioles were greatly decreased by the 2 treatments which limited the oxygen available to leaves (fig 3).

Endothall Inhibition of Transport. Maestri (17) observed that endothall [7-oxabicyclo(2.2.1) heptane-2,3-dicarboxylic acid] blocked both vein loading and transport of labeled assimilates in bean leaves. The present experiment was conducted to determine whether endothall, also, blocked the transport of $^{32}PO_4$ from blades into petioles.

Endothall at 5×10^{-3} M was sprayed on bean plants. One hour later the leaves were detached and 5 μl of solution containing $^{32}PO_4$ applied to the major veins of the blades. The leaves were placed in a moist chamber for 12 hours, freeze-dried, and only the petioles autographed. The blocking action of endothall on ^{32}P transport is clearly indicated in figure 4.

Discussion

Although Barrier and Loomis (1) described vein loading about 10 years ago, very little has been reported on it since. Recently, Maestri (17) observed that labeled assimilates were accumulated by veins of detached bean leaves; the loading was blocked by endothall, with the first appearance of callose being in the vein endings and border parenchyma. The blocking action of callose upon assimilate transport was discussed earlier by Webster and Currier (21).

Vein loading appears to be an oxygen requiring process. Kursanov (11) stressed the importance of metabolic energy for the transfer of assimilates from the mesophyll into the veins. Bauer (2) considered the main force in transport to be "pumps" in the leaves. Nelson (19) cited unpublished experiments of Mortimer which indicated that HCN blocked the flow of assimilates into the veins from the mesophyll of sugar beet leaves. It appears that factors which

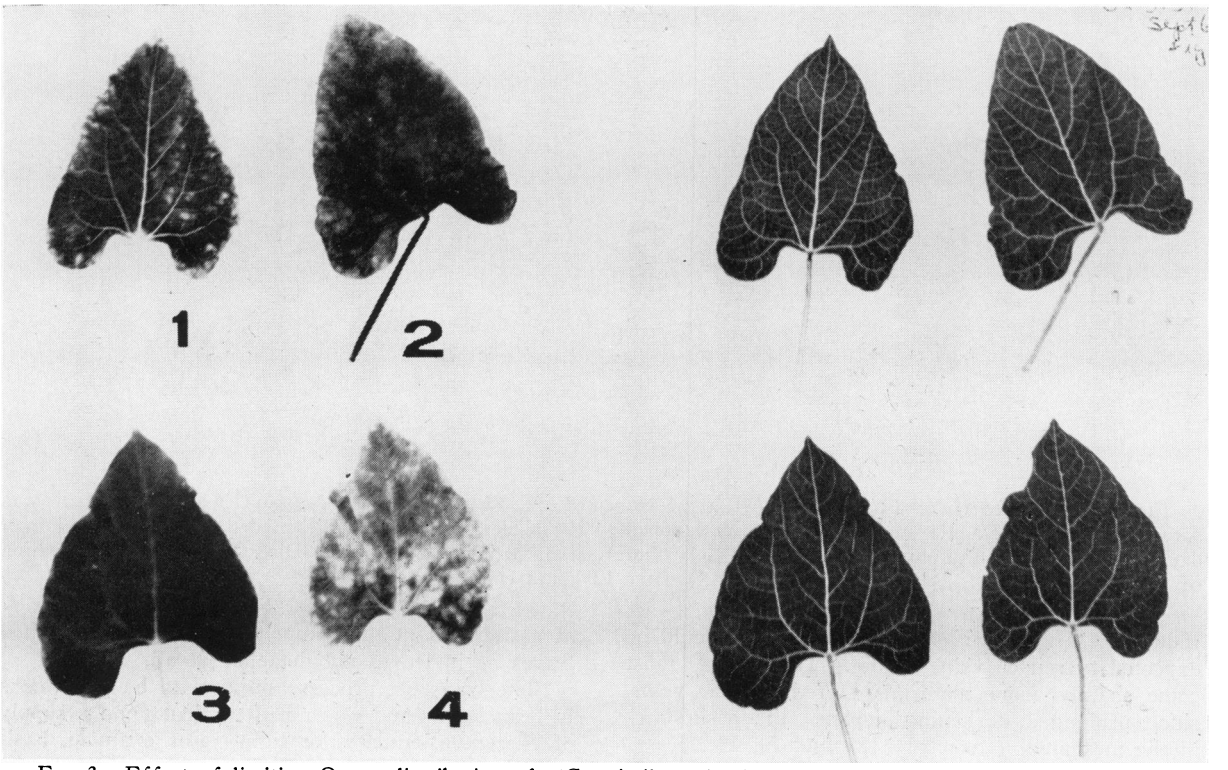

FIG. 3. Effect of limiting O_2 on distribution of ^{14}C-assimilates in detached bean leaves 6 hours after being exposed to $^{14}CO_2$ for 5 minutes. Autoradiographs on the left and mounted leaves on the right. 1) Initial distribution of radioactivity; 2) leaves stored in a dark moist chamber in air, petiole bases in water; 3) leaves as in 3, except in nitrogen gas; and 4) submerged in water in the dark.

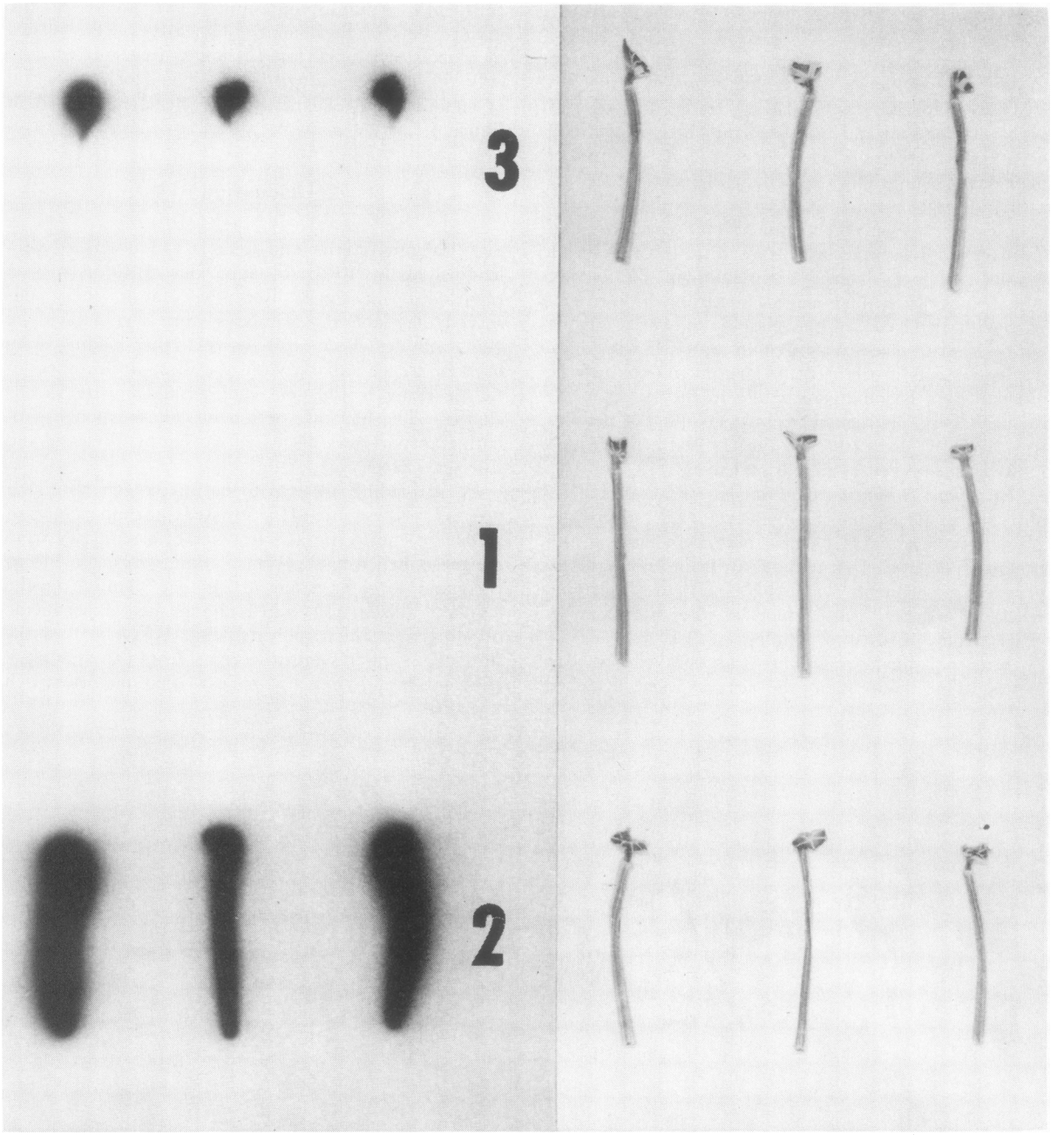

FIG 4. Effects of endothall at 5×10^{-3} on the transport of $^{32}PO_4$ in detached bean leaves. Endothall was sprayed on the plants and 1 hour later $^{32}PO_4$ was applied to the blades. Leaves were then detached and placed in a dark moist chamber. Autoradiographs on left and photograph of petioles on right. 1) Directly following application of $^{32}PO_4$, no endothall, 2) after 12 hours, and 3) after 12 hours endothall treated.

reduce the synthesis of high energy bonds would be expected to reduce vein loading. This energy must come mainly from materials stored in the veins, since prolonged darkening depletes the assimilates in the mesophyll [Leonard (12) and fig 1].

Detachment blocks the normal flow of assimilates out of leaves, causing them to become very concentrated in the veins and petioles (17). Prolonged detachment results in the mesophyll not being drained of assimilates quite as much as in freshly detached leaves or in leaves not detached at all.

The transport process appeared to be continuous in bean leaves and was not dependent upon a supply of current assimilates or light. For example, basipetal transport of $^{32}PO_4$ occurred in bean leaves removed from plants darkened for 8 days in the present experiment. In other studies Leonard and Glenn (16) observed vein loading and transport in

bean leaves that were detached and kept in the dark for 3 days prior to the application of labeled 2,4-dichlorophenoxyacetic acid, dicamba, or maleic hydrazide to the lamina. In contrast to our results on bean leaves, Hartt (8) considered that transport in sugarcane leaves was under photocontrol. Why transport should be under photocontrol in sugarcane leaves and not in bean leaves is not clear. We suggest that the truly polar and continuous aspect of transport is vein loading. Basipetal flow, on the other hand, is dependent upon a gradient in sink activity.

Although transport within detached bean leaves proceeded in a basipetal direction, some alteration was possible. Upward transport could be artificially induced by darkening the upper portion of the blade, cutting away the tissues on either side of the midrib or by treatment with benzyladenine (18). These treatments probably reduced the normal assimilate concentration in manipulated areas, thus causing upward transport into the treated areas. However, flow into the treated area was never sufficient to reduce basipetal transport visibly. Similar results were obtained with 2,4-D on assimilate transport (15). Evidently assimilates flow away from points where they are most concentrated. Bidirectional flow (upward and downward) is possible in a leaf, but unidirectional flow is the normal condition. Basipetal flow does not appear to be as strongly oriented in sugarcane blades as in bean blades. Hartt (8) found that basipetal flow could be inhibited by shading the upper part of the sugarcane blade. The veins in the upper and lower parts of these blades are of similar size, being in this respect different from those in bean blades. Her data suggest to us that the midrib is the strongest sink in sugarcane blades. Our autoradiographic results with Johnsongrass, also a member of the *Gramineae*, support this view.

Labeled assimilates within the petioles of the present experiment were confined mainly to the veins. From 50 to 66 % of the labeled sugars was sucrose, with the balance being glucose and fructose. Detached leaves of sugar beets were also found to accumulate these same sugars in the petioles (12). The occurrence of all 3 sugars in the petioles indicates that some sucrose moved out of the transport channels and was partially inverted in the phloem parenchyma (12, 23). Most results during the past 20 years support the conclusion that sucrose is the main form in which sugar is transported in most plants (22, 23).

Insofar as feasible, theories on transport should encompass what is thought to be known about the process. The authors would especially like to present the following items which should be considered in a theory. (1) Transport may or may not continue out of blades following periods of darkness. It was continuous in bean leaves but not in sugarcane blades (Hartt, 8). It is suggested that there was continuous loading of the veins in sugarcane blades as in bean blades and that this process is polar; however, longitudinal sink gradients in sugarcane blades are not as strongly developed as in bean blades. (2) Although transport was continuous in bean leaves, there was no evidence of any circulation. Thus labeled assimilates transported basipetally did not return sufficiently to label veins above the portion of the blade exposed to $^{14}CO_2$ (fig 2b, d, f, g). (3) The transport of previously produced assimilates out of a blade appeared to cease after 8 hours. Sucrose translocated by night in sugarcane (7) came largely from a conversion of storage compounds, *e.g.* organic acids, organic phosphates, and a glucose-xylose-glucuronic acid hemicellulose. Judging from the results of Leonard (13), only glucose and fructose, of the monosaccharides and sugar alcohols coming from the hemicellulose, would likely be converted appreciably into sucrose. (4) Assimilates imported into mature leaves (by darkening leaves treated with 2,4-D or benzyl adenine) were confined to the veins (15, 18); when similarly treated leaves were exposed to $^{14}CO_2$ in the light, assimilates were loaded into the veins. This evidence is interpreted as indicating that loading is centered in the margins of the veins, and vein endings. (5) Vein loading requires that the plasmodesmata in vein endings and border parenchyma remain open. Endothall (17) caused callose to form in these cells and, also, prevented vein loading. (6) Vein loading does not require large amounts of water or high turgor, since the process occurred in wilting leaves. (7) From item 6, it seems that transport channels must occupy a relatively small part of the space in a cell. Thaine (20) suggested the involvement of the endoplasmic reticulum in transport. Further evidence that there must be specific transport channels was indicated in the present work. Although most of the label in petioles was confined to the veins; about one-third of it consisted of glucose and fructose; however, only sucrose was present in the leachate from the petiole bases. Whether the sucrose came entirely from the sieve tubes or not is unknown; the leachate may have included sucrose coming from transport channels in other phloem cells. (8) The movement of virus particles between parenchyma cells through plasmodesmata (5) is suggestive of movement in a stream of water. Other substances could move in the same stream.

In order to reconcile the items mentioned above, a few suggestions on transport will be given. Pumps in the plasmodesmata of the cell walls separating the border parenchyma and the outermost phloem cells causes flow into the veins. The hydrostatic pressure created by pumping forces water into the cell walls, thus concentrating the solutions in the veins. The line of least resistance to flow is in the sieve tubes, in which substances flow to points of lower pressure (3), which are the sinks.

Specificity in what is loaded into veins could be a function of vacuolar participation, with substances in vacuoles being immobile (such as glucose and

fructose). Substances not readily confined by membranes might diffuse into the cell walls (like monuron, 3). Substances within the cytoplasm not bound to surfaces and small enough to pass through plasmodesmata (such as beet yellows virus, 5) would be subject to movement and accumulation by veins.

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