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Solution-Flow in the Phloem

II. PHLOEM TRANSPORT OF THO IN *BETA VULGARIS*[1]

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ABSTRACT

Translocation profiles along the path were studied using a modified flap-feeding technique for the simultaneous application of THO and ^{14}C-sucrose. A re-evaluation of a mathematical model for phloem transport with reversible lateral exchange of tracer along the path indicates that lower apparent velocities for THO as compared to labeled carbohydrate are primarily due to extensive lateral exchange of THO along the conduction path. Path-chilling experiments support the concept that THO and ^{14}C-sucrose exhibit different lateral exchange characteristics. The data presented are consistent with a solution-flow mechanism.

The mechanism underlying long distance transport of photosynthate has been a subject of controversy for many years (6, 21, 24). Points of contention center on the fine structure of the sieve tube, the extent and importance of metabolic energy, as well as the underlying driving potential which enables a source-sink system to function. The most prevalent of the proposed mechanisms is the mass-flow hypothesis adopted from Munch (14). Since mass-flow is set apart from some other proposed mechanisms by its requirement for a "bulk flow" of solution, many workers have looked to isotopic water as a tool in evaluating mass flow; however, experimental results have been contradictory.

Peel *et al.* (16), using aphids for collection of sieve tube contents of willow, demonstrated an apparent relative immobility of THO when supplied simultaneously with ^{14}C-carbohydrate and ^{32}P-phosphate. However, lateral loss of THO from the sieve tube could not be ruled out in those experiments. Similarly, Peel (15) indicates that H_2O is also relatively immobile in a longitudinal direction in willow. Biddulph and Cory (2) observed that THO was translocated, but with a lower apparent velocity than ^{14}C-sucrose. It is possible that the mobile THO exchanges freely with water in lateral tissues and with the upward moving xylem stream. Such an exchange would result in less recoverable radioactivity in THO. Gage and Aronoff (7) reported no significant export of THO when it was supplied with fructose to the leaf surface. Choi and Aronoff (4) found a negligible amount of THO along the path compared with T-photosynthate when tritiated water was supplied to the leaf as water vapor. Similarly, Trip and Gorham (22) noted that when THO and $^{14}CO_2$ were applied by painting and as a gas, respectively, no significant movement of THO was observed. However, when a flap-feeding technique was used for the simultaneous applications of THO and ^{14}C-carbohydrate, they could demonstrate the presence of parallel, almost flat, gradients in the petiole indicating concurrent export.

In the present investigations, the problem of "solution-flow" along the path is approached through the simultaneous application of THO and ^{14}C-sucrose using a flap technic adopted from Biddulph (1). The assumption that the lower apparent velocity reported for THO as compared with ^{14}C-carbohydrate is due to extensive lateral exchange and its subsequent "backwash" by the transpiration stream is evaluated with the aid of a modified mathematical model presented by Horwitz (12). Supporting evidence is supplied by experiments in which a cold block is used to alter flow and lateral exchange characteristics.

MATERIALS AND METHODS

Sugar beet plants (*Beta vulgaris* L., monogerm hybrid [SL 129 × 133] ms × [SP 6322-0]) were used at 6 to 8 weeks of age. Culture procedures were as described by Geiger and Swanson (11). Three- to 4-week-old plants were placed under incandescent light (14 hr light, 10 hr dark) which resulted in the elongation of petioles to a length of approximately 15 to 20 cm. The longer petioles enabled a large number of petiole samples to be taken. Plants were trimmed to a simplified source-sink system 24 hr before each experiment and placed in a low velocity fume hood and maintained under a normal photoperiod, except that illumination was provided via a 500-w water-filtered incandescent lamp providing 1200 ft-c to the leaf area.

Simultaneous feeding of 100 μc of ^{14}C-sucrose (10 mc/mmole) and 1 mc of THO (20mc/ml) was performed using the flap method. This method, modified after Biddulph (1), involves the feeding of tracer solution into a primary leaf vein in such a way as to allow the supplied THO and ^{14}C-sucrose to follow the "normal" xylary pathway for transpirational water. The kinetics and metabolic aspects of vein loading, following flap feeding, have been studied and found to be superior to other methods of tracer application (Sovonick and Geiger, in preparation). A first cut, 1 cm from the midrib, was made perpendicular to the long axis of the vein itself (Fig. 1). Cutting was done under water. The leaf blade was quickly raised from the water and the capillary tube (1.4 mm inner diameter × 75 mm) containing approximately 60 μl of tracer solution was placed over the trimmed portion of vein. It was found that uptake rates of bent or damaged bundles are reduced from

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1.0 to 1.5 μl/min to 0.5 μl/min or less. The blade was dissected in such a way as to confine the tracer to the blade area under study (see B, Fig. 1), which supplied one-seventh of the petiolar phloem (9). By limiting the feeding to a limited region of the blade base, it becomes easier to determine the velocity of translocation and to determine the specific radioactivity of the mesophyll pools supplying the "loading cells" of the minor vein (see 5 through 8 of Fig. 1). It has been observed (23) that the tracer is taken up through the xylem vessels and deposited in the mesophyll tissue; the translocate then enters the minor vein net work which in turn carries it to the primary vein, and finally to the sieve tubes of the petiolar phloem. There is apparently little anastomosing of the leaf traces in the upper two-thirds of the petiole and therefore little change in the conduit cross-sectional area (9, 10).

Following the labeling procedure, which lasted from 15 to 60 min, the petiole was quickly cut into 1-cm sections starting at the base. The first four 1-cm segments of the primary leaf vein proximal to the midrib were carefully dissected from the lamina and assayed. Each segment was extracted twice in 1.5 ml of 10% ethanol (v/v) at 0 C in a capped lyophilization tube. Following extraction, the tissue was removed from the solution, which was then shell frozen at −80 C. Five samples were then placed onto a lyophilization apparatus which contained individual water traps, maintained at −80 C (Dry Ice and acetone), for each of the samples. A secondary trap maintained at −196 C was initially used to determine whether significant loss of THO occurred; since no detectable loss occurred, the secondary trap was maintained at −80 C in later experiments.

After 1.5 hr of lyophilization, the residue, which was redissolved in 2 ml of 80% ethanol (v/v), and the condensate were added separately to 10 ml of dioxane containing 0.03% POPOP, 0.7% PPO, and 10% naphthalene (w/v). Radioactivity was assayed on a Beckman CPM-100 liquid scintillation spectrometer. Counting efficiency varied from 15 to 20% for tritium and from 45 to 55% for carbon 14 depending on quenching. All samples were corrected for quenching and counting efficiency which allowed radioactivity to be expressed in dpm.

Determination of the specific radioactivities of THO for the various tissues in Table I is based on the recoverable radioactivity as previously described and the estimated HOH content in various cell types. Total HOH for leaf punches was ascertained by determining the difference between fresh weight and dry weight of punches from the opposite side of the blade. Similarly, the water content of primary vein segments from the unlabeled side of the blade was determined on the basis of dry weights of segments which were corrected for 80% ethanol extracted solubles. On this basis, extracted 1-cm segments were dried, and their water content was estimated. The water content of individual cell types within the vein was estimated from a previous anatomical study (9).

RESULTS AND DISCUSSION

Distribution of THO and ^{14}C-Sucrose. An analysis of specific radioactivities for capillary fed lamina and exporting primary veins is given in Table I. For purposes of this paper, the lamina represents those portions of the leaf blade lying between the primary veins. Following a 30-min labeling period with THO and ^{14}C-sucrose, samples were taken as indicated in Figure 1. The specific radioactivity of THO in the interveinal mesophyll was higher than that in the phloem of the primary exporting vein which served it. This is the case whether it is assumed that all THO is localized in the sieve tubes alone or within all of the phloem cells. This situation might be expected if xylem water were used preferentially to mesophyll water in phloem transport and also if THO molecules were "washed out" of the bundle by transpiration. If one assumes that there is an efflux of xylem water into the interveinal tissue, one would expect THO in the blade bundles where loading of sieve tubes reportedly occurs to be continually washed out. This would, in effect, reduce the level of THO in the immediate vicinity of the loading cells; and if water is used in the bulk-flow of trans-

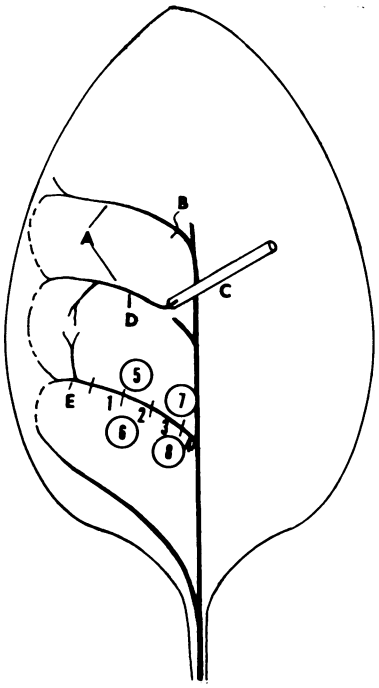

FIG. 1: Diagram of 10-cm blade showing feeding procedure and location of samples to be taken for tracer analysis. A: Primary veins; B: cut primary vein; C: feeding capillary; D: fed vein; E: exporting vein; 1-cm path segments 1, 2, 3, and 4; leaf punches 5, 6, 7, and 8. See also Table I.

Table I. *Specific Radioactivity of Lamina and Primary Vein Segments Following 30 Min of Flap Feeding with 1 mc of THO*

The specific radioactivity of the water was 10^{-5} dpm/mmole. See Figure 1 for distribution of samples in treated blade.

Specific Radioactivity of Lamina on Acropetal Side of Exporting Bundle (E); Leaf Punch 5 and 7, respectively	200		25	
Primary vein segment (1 cm)	1	2	3	4
Specific radioactivity assuming THO uniformly distributed throughout the vein	24.6	13.0	10.3	3.25
Specific radioactivity assuming THO localized in the phloem only	49.2	25.7	20.5	6.5
Specific radioactivity assuming THO localized in the sieve tubes only	147.7	77.7	61.5	19.5
Specific radioactivity of lamina on basipetal side of exporting bundle (E); leaf punch 6 and 8, respectively	47		23	

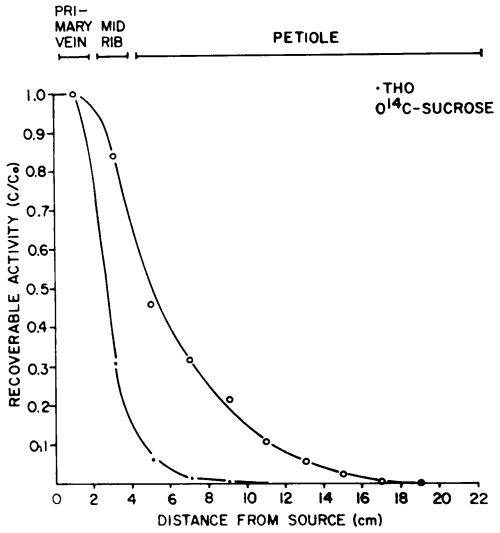

FIG. 2: Distribution profiles for THO and ^{14}C-sucrose following simultaneous feeding for 12 min.

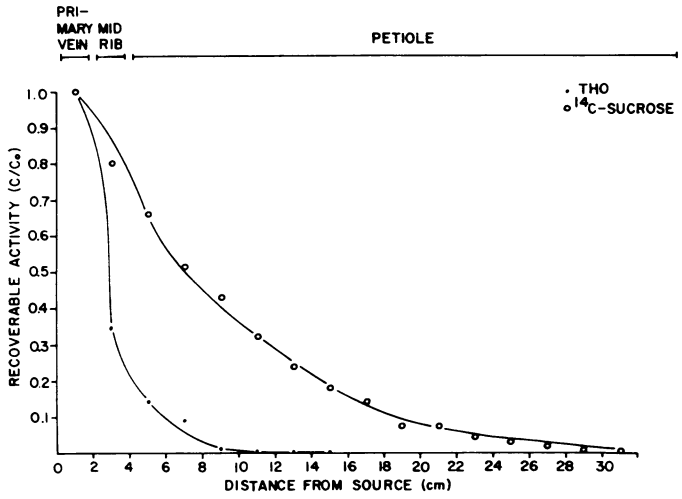

FIG. 3: Distribution profiles for THO and ^{14}C-sucrose following simultaneous feeding for 25 min.

locate, lower THO activities would be recovered along the path.

Figures 2 and 3 demonstrate typical distribution profiles following 12 and 25 min of simultaneous labeling with ^{14}C-sucrose and THO. In all, 30 replicate experiments of this general type were carried out. The profiles are obtained by plotting radioactivity ratios (C/C_0) of THO and ^{14}C-sucrose *versus* distance (x) along the path. The radioactivity ratio (see also ref. 3), C/C_0, is determined from the recoverable activity in a given unit length of path (C) and the recoverable radioactivity at a point $x = 0$ (C_0). The segment used in determining C_0 was dependent on the length of the exporting primary vein basipetal to the fed vein (where not specified, segment 3 of Fig. 1 was used) and represented the primary vein segment distal to the midrib. The THO profile typically lags behind that of ^{14}C-sucrose. The apparent velocities for the two tracers in the 12-min experiment are 54 and 102 cm/hr, respectively; and in the 25-min experiment 35 and 72 cm/hr, respectively. Since a mass-flow or "solution-flow" mechanism requires that solvent and solute, once in the conduit, travel concurrently at the same velocity, it is necessary to account for the deviation in solvent and solute velocities. This deviation may be due to one or more of the following factors: (*a*) differences in the penetration time from mesophyll or epidermis to the phloem, depending on application method; (*b*) differences in the kinetics of equilibration of individual tracer moieties with their respective unlabeled pools; (*c*) dilution of THO activity in the vicinity of the loading phloem by the outward moving unlabeled xylem stream; (*d*) extensive lateral exchange of THO with unlabeled tissue water and eventual back wash as the diffusing THO molecules come in proximity with the upward moving xylem stream.

In earlier studies on the simultaneous transport of isotopically labeled water and photosynthate (2, 4, 7) the generated profiles were similar to those in Figures 2 and 3. From the tracer distribution along the path, it is evident that solution-flow is not occurring since the solute and solvent show different apparent velocities. However, such tracer profiles may still describe a solution flow if lateral loss of THO from the sieve tube is much greater than the lateral loss of ^{14}C-sucrose.

Biddulph and Cory (2), on application of THO and ^{14}C-carbohydrate to the leaf lamina of red kidney bean, found that THO exhibited a lower apparent velocity than that for ^{14}C-photosynthate, 86.5 and 107 cm/hr, respectively. A comparison of the moles of THO and labeled sucrose translocated from the leaf per mole supplied demonstrated that 100 times more ^{14}C-sucrose was loaded and exported. Although "solution-water" was found along the translocation path, they expected to find 40 times the radioactivity actually recovered, if a solution-flow were occurring. Gage and Aronoff (7) studied the distribution of THO and T-photosynthate along the translocation path of soybean following equilibration of the blade with THO vapor in the dark. Because they did not observe any significant export of THO, but some export of tritium in the form of tritiated sugar, they interpreted the results as negating the mass-flow hypothesis. They considered the discrepancy between these data and those of Biddulph and Cory (2) as possibly being the result of differences in hydrostatic conditions between the two plant systems. Choi and Aronoff (4), feeding with THO vapor, failed to demonstrate parallel transport of THO and T-photosynthate from the supply leaf. They interpreted the lack of recoverable THO activity along the path as possibly resulting from extensive lateral exchange of the tracer moiety with unlabeled tissue water. Using a mathematical model proposed by Horwitz (12), they did not account for the deviation between predicted and experimentally observed THO activity based on lateral exchange. Choi and Aronoff supplied 200 μc of THO vapor to a 4-cm length of soybean stem. After 35 min, 44% of the absorbed THO was exported acropetally in the xylem stream. It is clear, therefore, that xylem back wash is a significant factor in the distribution of THO along the transport path and may, therefore, have affected their mathematical analysis.

A re-evaluation of Horwitz's model (12) has been undertaken and described in the preceding paper (3). Briefly, the model predicts the distribution of tracer down the path from a point $x = 0$ following a time (t); at the point $x = 0$ along the path, the concentration of tracer remains constant. If the concentration at $x = 0$ is set equal to unity, then the model generates a profile in terms of concentration ratios, C/C_0, where C is the recoverable activity in a given unit-length of path and C_0 is the activity at $x = 0$. When comparing theoretical to experimental profiles, the latter are greatly affected by the activity of THO at $x = 0$ (C_0).

Choi and Aronoff (4) estimated the value of C_0 from the radioactivity of the supplied THO and the total water content of the blade. Table I shows the distribution of THO in a loaded primary vein and its surrounding lamina (see Fig. 1). It is clear that the specific radioactivity of THO in the primary

vein, irrespective of specific cell types which may contain the tracer, is lower than that of the surrounding lamina. For this reason, the profiles in this study have been compiled by selecting C_0 as the THO activity recovered from the 1-cm section of primary vein immediately basipetal to the feeding area (Fig. 1). This procedure was adopted to minimize the discrepancy which exists between the supplied specific radioactivity of THO and ^{14}C-sucrose, and that which is made available for export due to dilution in endogenous pools. The selection of segment 1 in Figure 1 was based on previous anatomical data (9) demonstrating a relatively constant sieve tube area for primary leaf veins and their bundle traces in the petiole.

Since this model involves the evaluation of a number of variable plant parameters (velocity, v; area of lateral sink tissue, A_t; area of the translocation path, A_p; time of transport, t; and a diffusional permeability constant, k), its value in elucidating the mechanism of translocation depends on an accurate determination of the above parameters. Velocity was determined by calculation of the distance ^{14}C-sucrose had traveled in short term experiments (Figs. 2 and 3) or by the arrival time at a target leaf (Figs. 4 and 5). In most cases, these apparent velocities fall between 48 and 72 cm/hr for carbohydrate, which is within the normal range for this plant as measured in several ways (11). Anatomical data (A_p,A_t) were obtained from plants of the same cultivar and grown under similar conditions (9) and agreed closely with anatomical measurements of Sokolova (17) for *Beta vulgaris*. The duration of the labeling period (t) represents the time from application of the feeding capillary to the time of sampling. The diffusional permeability coefficient (k) is based on the osmotic permeability coefficient determined by Stadelmann (18) for *Beta vulgaris* hypocotyl, which according to the work of Miftakhutdinova and Gusev (13) is of the correct magnitude. According to Stein (19), the diffusional permeability coefficient will be no smaller than one-half of this osmotic permeability coefficient.

It is useful to compare the models of THO transport by self-diffusion (4) and mass flow with reversible exchange to the experimental data. Figures 4 and 5 represent THO distribution along the translocation path, assuming self-diffusion with no exchange (curve C) or mass flow with reversible lateral exchange (curve B), compared with the experimentally

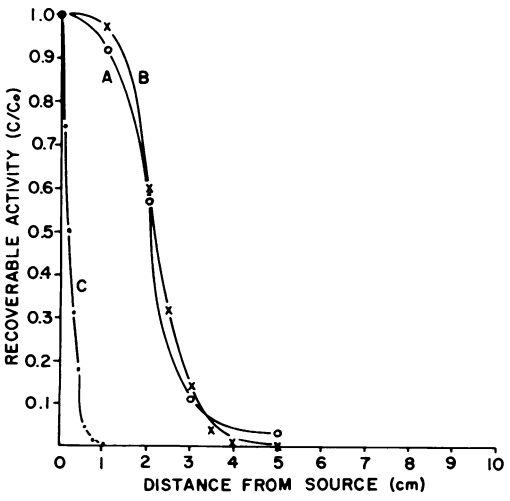

FIG. 4: Comparison of THO distributions (C/C_0) as a function of distance along the translocation path. Curve A: Experimentally determined radioactivity ratios following 30 min of labeling; curve B: mass-flow model with reversible exchange of tracer, assuming v = 590 mm/hr, t = 0.5 hr, k = 0.0339 mm²/hr, A_t = 0.0012 mm², and A_p = 0.0000667 mm²; curve C: self-diffusion, assuming D = 8.784 mm²/hr, and t = 0.5 hr.

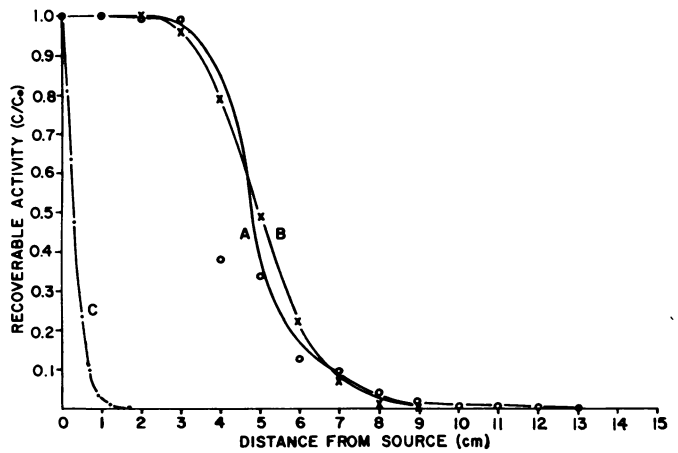

FIG. 5: Comparison of THO distribution (C/C_0) as a function of distance along the translocation path. Curve A: Experimentally determined radioactivity ratios following 60 min of labeling; curve B: mass-flow model with reversible exchange of tracer, assuming v = 850 mm/hr, t = 1.0 hr, k = 0.0339 mm²/hr, A_t = 0.00112 mm², and A_p = 0.0000667 mm², curve C: self-diffusion, assuming D = 8.784 mm²/hr, and t = 1.0 hr.

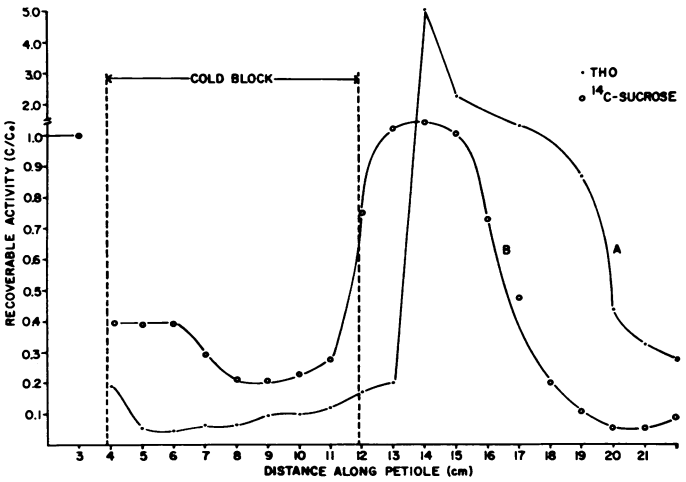

FIG. 6: Distribution of THO and ^{14}C-sucrose following simultaneous labeling for 40 min. An 8-cm segment of the petiole was cooled to 1 C for 1.5 hr prior to and during labeling. Curve A: THO; curve B: ^{14}C-sucrose.

determined activities (curve A) for 30 and 60 min of labeling, respectively. The model for mass-flow fits the experimental data much better than does that of a self-diffusion mechanism. Considering that mathematical models are seldom precise in their evaluation of a natural process, a closer fit between experimental and calculated results should not be expected. The leading edges of the experimental curves contain a slightly higher radioactivity than predicted. This could be explained by the protonation and hydration of the carbohydrate molecules. The deviation in slope is most likely the result of parameters not evaluated in the model, such as back wash of THO by the xylem stream.

Cold Blocks. A further test of the mass-flow model is obtained by varying the temperature along the upper portion of the petiole, thereby reducing permeability coefficients. Sugar beet exhibits a rapid and sustained recovery of translocation during path chilling at 1 C (8, 20) and would therefore be useful in studying the effect of lateral exchange of THO and carbohydrate from the translocation path to its surrounding tissues. Figure 6 is representative of distributions for THO and

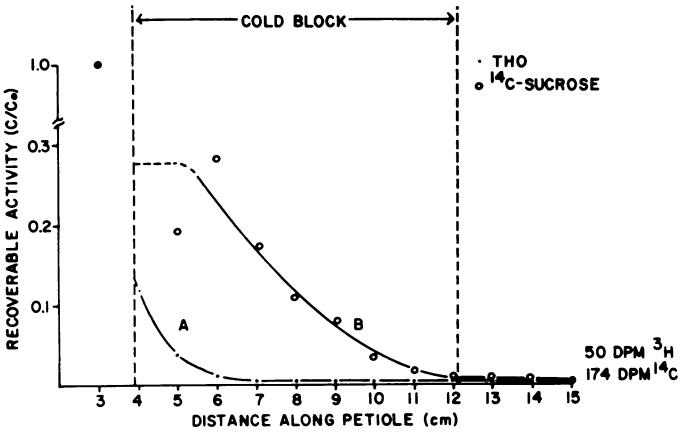

FIG. 7: Distribution of THO and ^{14}C-sucrose following simultaneous labeling for 10 min. An 8-cm segment of the petiole was precooled at 1 C for 1.5 hr prior to and during labeling. Curve A: THO; curve B: ^{14}C-sucrose.

^{14}C-sucrose obtained with simultaneous feeding for 90 min following normal recovery from a 1 C cold block. Several characteristics of these tracer distribution plots warrant mentioning. In comparing the radioactivity for ^{14}C-sucrose and THO recovered per unit length of the chilled and unchilled portions of the path, it is evident that the chilled portion contains approximately one-twentieth the THO activity as compared with the unchilled region. Similarly, the path segments in the cooled region contain one-third the ^{14}C-sucrose activity of the unchilled portion. The reduction in radioactivity within the cold block results from a decrease in the extent of lateral leakage for both THO and ^{14}C-carbohydrate. The decrease in lateral loss of THO in the cooled zone is probably the result of a reduction in the diffusional permeability coefficient (5, 19). Evidence for the lateral leakage or metabolic removal of carbohydrate from the path has been considered in the literature (9, 10). An obvious effect of the lateral loss of ^{14}C-carbohydrate from the translocation path would be to lower the apparent velocity (v) used in the mathematical model for THO distribution along the path. However, based on theoretical plots using Horwitz's model (3, Fig. 2), it can be assumed that moderate changes in velocity of 10 to 20% would have a minor effect on the over-all distance THO would travel along the path with time.

In the uncooled portion of path below the cold block, an increased accumulation of tracer is evident; the apparent accumulation of THO is five times that of ^{14}C-sucrose. This would suggest the presence of an extensive lateral sink for THO. A further aspect to be noted is that THO has moved a distance greater than 22 cm down the path. From theoretical plots of Horwitz's model (3, Figs. 2 and 3), assuming a velocity of 600 to 900 mm/hr and a translocation time of 90 min, THO activity should be recoverable approximately 9 to 12 cm from C_0; yet it is found significantly further than this distance in Figure 6 (curve A). This would support the contention that differences in the apparent velocities for THO and ^{14}C-carbohydrate, following simultaneous feeding, may be dependent on the rate of lateral loss and the extent of the lateral sink.

If discrepancies in apparent velocities of THO and tracer carbohydrate are in fact due to extensive lateral loss or exchange, it becomes possible to simulate a translocation path with relatively little lateral loss capabilities. An 8-cm cooling jacket is placed immediately basipetal to the blade and cooled to 1 C for 1.5 hr. At this time, normal translocation has recovered, a feeding capillary containing THO and ^{14}C-sucrose is applied in the usual manner, and the plant is allowed to translocate for 10 min. Figure 7 represents the distribution obtained at a point 15 cm from the primary exporting vein; 50 dpm ^{3}H and 175 dpm ^{14}C were recovered. Although the curves A and B are quite dissimilar, possibly due to the 6 cm of path ahead of the cold block where backwash and lateral exchange of tracer undoubtingly occur, the confluence of the THO and ^{14}C-sucrose plots does demonstrate concurrent transport. In effect, the reduction in loss of THO from the translocation path (*i.e.*, sieve tubes) has resulted in concurrent transport. Under normal conditions (*i.e.*, uncooled tissue), detectable levels of THO should not have been found beyond 4 to 6 cm of path following 10 min of labeling (3, Fig. 3), yet with a cold block in place THO activity ($C/C_o = 0.01$) was recoverable 15 cm from the point of application. In all of these experiments, ^{14}C-sucrose was exported to a greater extent than was THO. This may result either from differential transport velocities within the leaf mesophyll, or from other factors such as xylary dilution of THO at the phloem loading sites.

The effect of extensive lateral exchange of THO from the translocation stream and its back-wash by the upward moving xylem stream necessitates a re-evaluation of phloem transport data involving the use of THO. A mathematical model constructed on the basis of exchange phenomena generated theoretical THO profiles which showed a good correlation to those experimentally determined. The characteristically lower apparent velocities of THO as compared to ^{14}C-carbohydrate are thought to be the result of the above phenomena. Cold block studies demonstrate the existence of extensive lateral loss of both THO and ^{14}C-carbohydrate from the translocation path to the surrounding tissues. The results support a solution-flow mechanism of phloem transport in sugar beet.

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