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Translocation and Accumulation of Translocate in the Sugar Beet Petiole[1]

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Abstract. Accumulation of translocate during steady-state labeling of photosynthate was measured in the source leaf petioles of sugar beet (*Beta vulgaris* L. monogerm hybrid). During an 8-hr period, 2.7 % of the translocate or 0.38 μg carbon/min was accumulated per cm petiole. Material was stored mainly as sucrose and as compounds insoluble in 80 % ethanol. The minimum peak velocity of translocation approached an average of 54 cm/hr as the specific activity of the $^{14}CO_2$ pulse was progressively increased. The ratio of cross sectional area required for translocation to actual sieve tube area in the petiole was 1.2. A regression analysis of translocation rate *versus* sieve tube cross sectional area yielded a coefficient of 0.76. The specific mass transfer rate in the petiole was 1.4 g/hr cm² phloem or 4.8 g/hr cm² sieve tube. Histoautoradiographic studies indicated that translocation occurs through the area of phloem occupied by sieve tubes and companion cells while storage occurs in these cells plus cambium and phloem parenchyma cells. The ability of the petiole to act as a sink for translocate is consistent with the concept that storage along path tissue serves to buffer sucrose concentration in the translocate during periods of fluctuating assimilation.

In rosette plants such as sugar beet the petiole constitutes a major path for translocation. Previous studies have shown that the path also serves as a sink for translocate (1, 4, 8, 10, 11, 13, 14). Several workers have suggested that accumulation along the translocation path helps maintain the solute concentration in the sieve tube sap during periods of fluctuating assimilation (10, 14). The rate of lateral movement of translocate out of the sieve tubes is of interest in evaluating the extent of storage along the path, in formulating translocation models (4), and in interpreting translocation profiles (2).

The present study of the sugar beet petiole was undertaken to compare mass transfer and accumulation rates in the petiole and relate these to structural features in the petiole. Measurements of mass transfer rate, translocation velocity, and sieve tube cross section were used to compare the available cross sectional area with that calculated to be required for conduction of translocate at a concentration determined by exudate analysis (5). Freeze-dry histoautoradiography was used to locate sites of accumulation and channels of translocation. The correlation of physiological and anatomical measurements from the translocation path attempted in the present study is useful in evaluating various proposed translocation mechanisms.

Materials and Methods

Plant Material. Sugar beet plants [*Beta vulgaris* L., monogerm hybrid (SL 129×133) MS X SP6322-0] were grown by solution culture in controlled environment cabinets as described previously (6). Plants were selected for uniformity of size and morphology from 5- to 6-week-old plants, pruned to include a single source leaf and a single expanding

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sink leaf. Source-leaf area of the 13 plants used for accumulation studies averaged 0.50 ± 0.07 dm^2 and the translocation rate was 25.6 ± 7.6 μg C/min dm^2 leaf blade.

Measurement of Accumulation. Photosynthate was labeled by steady-state labeling procedures described earlier (7). Following various periods of translocation of ^{14}C-labeled photosynthate the plant was divided into source blade, petiole, sink leaf, crown and roots. The sink portions of each plant exclusive of the source-leaf petiole were wet-oxidized to CO_2 and the radioactivity was assayed with a Nuclear Chicago Dynacon ion chamber system (6). The petiole was divided into two 3-cm segments, 1 distal and 1 basal to a 1-mm mid-section taken for cytological study. Each large segment was assayed separately for materials insoluble in 80 % (v/v) ethanol and for sucrose, by soxhlet extraction followed by paper chromatography and wet oxidation of the various fractions (6). After attainment of isotopic saturation of sucrose in the blade, which occurs after about 100 min of labeling, the amount of carbon derived from the translocate was calculated by multiplying the amount of radioactivity present by the specific activity and an isotope effect factor of 1/0.85 (8). Although individual measurements of accumulated translocate will be low by the constant, small amount accumulated prior to attainment of isotopic saturation, the slope of the time course curve constructed from these points will be a valid measure of rate.

Histoautoradiographic Procedures. Cross sections of petiole were prepared for histoautoradiography by a modification of the procedures of Branton (12). Material was sampled after 60 min of steady-state photosynthesis, at which time an estimated 55% of the radioactivity in the petiole was in transit (Fig. 2).

Histological Procedures. At the end of each experiment, a 1-mm section was removed from the middle of the petiole and fixed in 3 % (v/v) glutaraldehyde in pH 7.2, 0.15 M sodium phosphate buffer. Paraffin sections, 6 μ thick, were stained by the tannic acid-resorcin method of Cheadle *et al.* (3) and photographed. The area of a vascular bundle occupied by xylem, and by each cell type of the phloem was determined by weighing the traced area of each vascular component drawn from photographs. Areas were corrected for shrinkage during preparation, by measuring scaled photographs of sections from fresh and from embedded tissue.

Results and Discussion

To determine the extent to which the petiole of a 10-cm sugar beet leaf functions as a sink for translocate, 13 plants were analyzed for ^{14}C-compounds after varying periods of steady-state labeling with $^{14}CO_2$. The amount of ^{14}C-translocate accumulated in various categories of compounds in the petiole is summarized in table I. Translocate reaches 90 % of isotopic saturation after about 80 min of labeling and from this time, slopes of accumulation are a valid measure of mass transfer into the various pools. Of the 14.2 ± 4.3 μg C in transit in a 1-cm segment of petiole, 2.7 ± 1.0 % or 0.38 ± 0.14 μg

Table I. *Accumulation of Translocate Along Petiole of Sugar Beet Plants Measured During Steady State Labeling of Photosynthate*

Translocation period	Total labeled material per length of petiole	Accumulated translocate per length of petiole	Rate of accumulation of translocate in petiole[1]	Proportion of translocate stored in petiole per min	Translocation rate through petiole	Translocate moving through a length of petiole[2]
min	*μg C/cm*	*μg C/cm*	*μg C/cm min*	*%*	*μg C/min*	*μg C/cm*
120	30.8	20.5	0.41	4.0	9.3	10.3
150	71.7	50.7	0.63	3.0	18.9	21.0
180	78.6	65.2	0.59	4.4	12.1	13.4
210	53.3	35.4	0.25	1.4	16.1	17.9
240	60.4	52.2	0.31	3.7	7.4	8.2
270	51.7	40.2	0.20	1.8	10.4	11.5
300	96.9	84.0	0.37	2.8	11.6	12.9
330	56.3	41.5	0.16	1.1	13.3	14.8
360	115.0	101.9	0.35	2.7	11.8	13.1
410	101.8	93.4	0.27	3.3	7.6	8.4
420	201.0	182.3	0.52	2.8	16.8	18.7
450	175.5	162.4	0.43	3.3	11.8	13.1
480	195.9	173.9	0.42	2.0	19.0	21.1
M ± S D	...	...	0.38 ±0.14	2.7 ± 1.0	12.8 ± 3.9	14.2 ± 4.3

[1] Time calculated using 70 min as apparent time zero to correct for delay in attaining isotopic saturation.
[2] Based on a velocity of 0.9 cm/min.

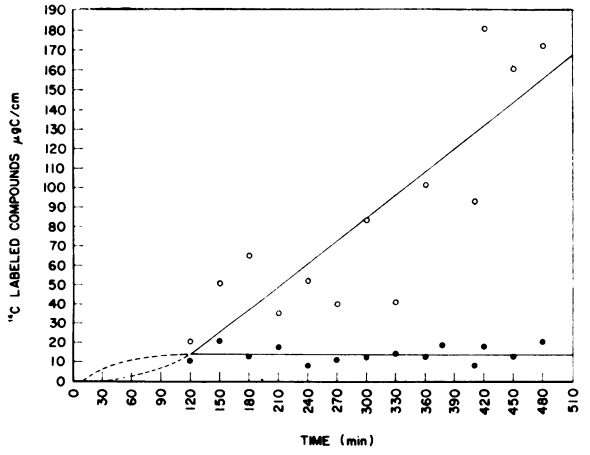
C/min•cm is accumulated in the petiole. Because of the delay of ^{14}C-translocate in reaching isotopic saturation, this latter slope (Fig. 1) has a time axis intercept at 70 min; this time intercept was used to calculate accumulation rates. At this stage of development the petiole is an active sink, constituting 8 to 10 % of the sink tissue on a fresh weight basis while containing approximately 18 % of the material accumulated in the sinks (table II). Using a mathematical model for translocation in soybean, Evans and Ebert (4) found lateral loss from the sieve tubes to amount to 0.8 % per min, about 30 % of the value we observed in sugar beet. A comparison of data for individual petioles reveals considerable between-plant variability in accumulation rates even though the plants were selected for uniform external morphology. The sink leaf, crown and roots show less variability in this regard than the petiole. Variations in petiole accumulation rate showed no apparent correlation with external morphology of the petiole, cross-sectional area of sieve tubes, extent of the phloem, or degree of cambial activity. Hoad and Peel (11) investigated the effect of carbohydrate status and of the presence of various solutes on the rate of solute removal along the translocation path. Their findings indicate that a variety of factors in addition to morphology, such as solute concentration in the xylem, affect accumulation rate in the petioles and are presumably responsible for the variability noted in the present study.

The time course for translocate accumulation in the petiole is shown in Fig. 1. A regression line was drawn on the assumption that accumulation of ^{14}C-translocate proceeds at a uniform rate following an initial isotopic equilibration period. The predominance of net accumulation over exchange of labeled translocate is indicated by the absence of a gradual decline in rate which is characteristic of exchange phenomena. Mortimer (13) found that the decline in ^{14}C in a sugar beet petiole slowed after about 2 hr, at which time nearly 25 % of the peak activity remained, presumably stored along the path. Various workers have concluded that the stem and petiole may serve as sites for storage of translocate during peak assimilation periods, with remobilization of these reserves during periods of low productivity (8, 10, 14).

Table II. *Pattern of Distribution of ^{14}C Translocate in Various Sinks of Sugar Beet Plants During Steady State Labeling of Photosynthate*

	Duration of ^{14}C labeling	^{14}C in petiole	^{14}C in sink leaf	^{14}C in crown and roots
	min	%	%	%
	120	20.3	25.7	54.0
	150	22.1	26.8	51.1
	180	38.2	13.9	47.6
	210	14.5	11.7	73.9
	240	21.0	20.0	59.0
	270	12.7	23.1	64.2
	300	15.4	28.2	55.5
	330	9.1	16.9	73.9
	360	16.9	19.4	63.7
	410	16.2	17.7	66.1
	420	19.7	11.9	63.2
	450	18.5	17.1	64.3
	480	13.8	15.3	71.2
M ± S D	...	18.3 ± 7.0	19.1 ± 5.5	62.1 ± 8.4

Distribution of radioactivity among various categories of compounds is summarized in the data of table III. Compounds insoluble in 80 % ethanol form a constant proportion of the ^{14}C-translocate stored in the petiole, making up 30.5 ± 9.8 % of the total (Fig. 2). The labeled soluble fraction,



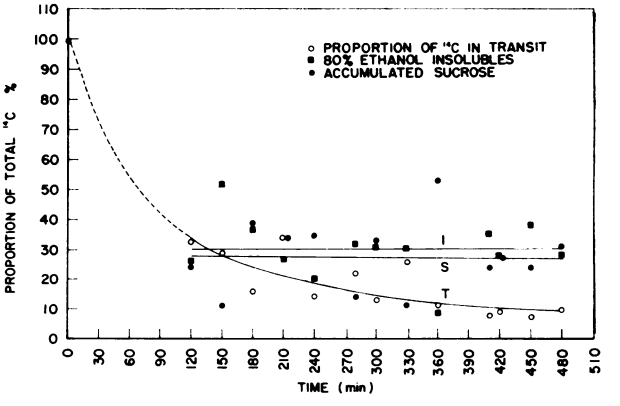


FIG. 1. (left) Labeled translocate (●) and accumulated labeled translocate (○) present in a unit length of petiole of a 10-cm sugar beet leaf during steady-state labeling of photosynthate.

FIG. 2. (right) Proportion of labeled translocate in the petiole in transit (○) in labeled accumulated sucrose (●) and in labeled compounds insoluble in 80% ethanol (■) during steady-state labeling of photosynthate.

Table III. *Distribution of ^{14}Carbon in Petiole of Sugar Beet After Various Periods of Steady-State Labeling of Photosynthate*

Labeling period	80 %-Ethanol insoluble material		Total sucrose		Accumulated sucrose	Proportion of sucrose in transit[2]	Proportion of label in petiole which is in transit
min	*μg C/cm*	%[1]	*μg C/cm*	%[1]	%[1]	%	%[1]
120	8.2	26	18.1	59	25	57	33
150	37.3	52	29.0	41	11	73	29
180	29.4	37	36.3	46	38	17	16
210	14.3	27	20.1	38	34	89	34
240	11.8	20	29.7	49	35	28	14
270	16.3	32	18.9	37	14	61	22
300	30.4	31	41.6	46	32	31	13
330	17.3	31	21.1	38	11	70	26
360	10.1	9	75.1	65	53	18	11
410	37.4	36	32.8	32	24	26	8.3
420	57.1	28	75.4	37	28	25	9.3
450	67.7	39	54.8	31	24	24	7.5
480	57.4	29	82.1	42	31	26	10
M ± S D	...	30.5 ± 9.8	...	...	27.7 ± 11.7	...	...

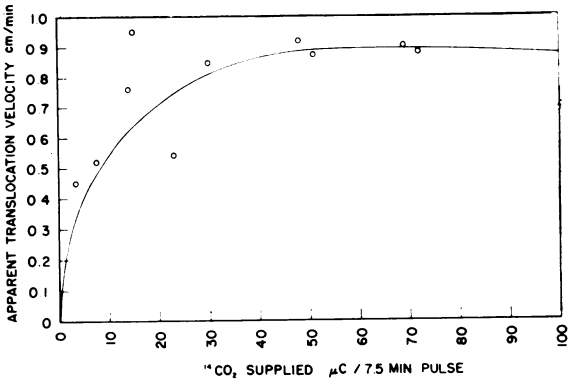
[1] Based on total ^{14}C in petiole.
[2] Based on assumption that translocate is predominantly sucrose.

which includes compounds in transit in addition to those stored along the path, changes composition with time. Sucrose constitutes a major portion of the 80 %-ethanol soluble fraction, ranging from up to 90 % after 120 min to approximately 50 % after 300 min. From the data in table III it can be seen that, throughout the labeling period studied, the proportion of ^{14}C-sucrose in transit decreases while the proportion accumulated outside the translocation stream remains constant at approximately 28 % (Fig. 2). These data indicate that in the petiole, sucrose and 80 %-ethanol insoluble compounds are equally important as stored materials derived from translocate. Glucose, fructose, malic acid and some amino acids comprise the remainder of the soluble fraction. The ratio of radioactivity in the upper and lower 3-cm petiole segments was found to be 0.89 ± 0.43, with no indication of a logarithmic profile during the 120- to 480-min translocation period. The steep profile found in pulse-labeling experiments (13) apparently results from exchange by the advancing front as well as from the time course of the ^{14}C-pulse.

Part of the present study was devoted to relating mass transport rate and accumulation rate to structural measurements in the petiole. A section from the middle of each petiole was examined to determine the cross sectional area of various phloem components in a plant whose mass transfer rate was known. Comparison of the actual and theoretical cross sectional areas for conduction requires measurement of the translocation velocity, the concentration of the sucrose in transit, the cross section of the sieve tubes and the mass transfer rate. The rationale of correlations of this kind is discussed by Canny (2).

A number of authors have discussed the difficulties in measuring and in interpreting translocation velocity measurements (2, 13, 16). The method chosen for this study consisted of administering a pulse of $^{14}CO_2$ to a photosynthesizing leaf and observing the time required for the labeled translocate to arrive at the sink leaf. The time used in the calculation of velocity includes the time required for uptake of the labeled photosynthate by the translocation system in addition to the transit time. Mortimer (13) found ^{14}C sucrose in the midrib of the sugar beet leaf only 2 min after the start of $^{14}CO_2$ labeling, indicating that this time of entry is short.

An inherent problem in velocity studies is the delay in observing radioactivity while it is below the detection threshold. To study whether this delay introduces serious error, $^{14}CO_2$ of increasing specific activity was used in the velocity experiments. The apparent velocity was calculated using the distance from the base of the source blade to the center of the sink leaf and the time from the start of labeling until the first detection of radioactivity. When low-specific-activity $^{14}CO_2$ was used, the rise-time of the pulse front was comparatively long, resulting in a long delay before the detection threshold in the sink was exceeded. With increasing specific activity, the apparent velocity increased and asymptotically approached a limit (Fig. 3). It appears that a pulse of at least 50 μc/7.5 min produced a pulse front whose slope increased rapidly enough to give a valid estimate of the minimum translocation velocity.



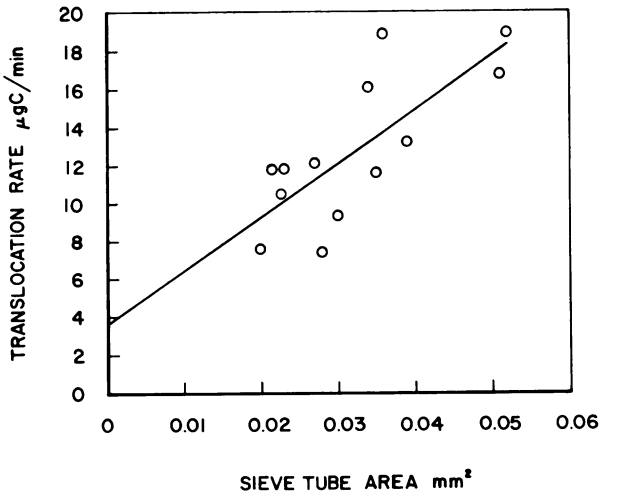


FIG. 3. (left) Apparent translocation velocity as a function of the amount of ^{14}C present in the 7.5 min labeling pulse. Maximum possible label using carrier free $^{14}CO_2$ was approximately 3800 μc/pulse.

FIG. 4. (right) Correlation between mass transfer rate and sieve-tube cross-sectional area in the petiole of a 10-cm sugar beet leaf.

The velocity measured in this study is the minimum velocity of the fastest moving translocate or, as discussed by Zimmerman (16), the minimal peak velocity rather than a true average velocity. The observed velocity of 54 cm/hr is of the same order as the apparent velocity of 50 to 135 cm/hr reported by Mortimer for sugar beet petioles (13).

The sugar concentration of phloem exudate from the blade end of a severed petiole was found to be approximately 8 % (w/v). Analysis of the exudate by paper chromatography followed by autoradiography, revealed that the only sugar observed was sucrose which contained practically all of the detectable radioactivity. Because it was difficult to sample the exudate consistently, the value of 8.8 % (w/v) sucrose reported by Fife, Price and Fife (5) for the sugar beet phloem exudate was used in the calculations given below.

To calculate the theoretical cross-sectional area required for the observed mass transfer rate, the total amount of sucrose in transit in 1 cm of petiole was divided by the concentration of sucrose per cm^3 sap. In table IV, values for the required cross section are compared with the areas for phloem and for sieve tubes in the respective petioles. The average ratio of required to actual sieve-tube cross-sectional area of 1.2 indicates that sieve tubes throughout the phloem area are functional. The large departures from the average for some plants probably reflect deviations from average values for the velocity and sucrose concentration which were used to calculate the required area.

Although plants were selected for external uniformity, there was considerable deviation in translocation rate. A plot of translocation rate as a function of sieve-tube cross-sectional area is shown in Fig. 4. Statistical analysis yielded a value of 0.76 for the correlation coefficient indicating a high degree of correlation. Sieve tubes occupied 29.0 ± 3.2 % of the area of phloem exclusive of the phloem fibers. Companion cells occupied 15.8 ± 4.5 % of the cross section while phloem parenchyma cells occupied the remaining 55.1 ± 7.0 %. A study of the cross sectional area of vascular components at various levels in the leaf revealed that the total area of phloem was substantially the same in major veins of the lamina and throughout the petiole (table V).

The specific mass transfer rate for the 13 plants studied averaged 1.40 g/hr•cm^2 phloem exclusive of fiber cells or 4.8 g/hr•cm^2 sieve tube area. Canny (2), in a summary of previous specific mass transfer studies, reported an average value of 0.65 g/hr•cm^2 phloem or 3.3 g/hr•cm^2 sieve tube for petioles. Assuming 20 % of the phloem to be sieve tubes, Zimmerman (16) reported a value of 6 to 18 g/hr cm^2 of sieve tube for specific mass transfer in white ash.

Freeze-dry autoradiography of petiole cross sections was undertaken with plants sampled after 60 min of steady-state labeling with $^{14}CO_2$. At that time, approximately 55 % of the ^{14}C was estimated to be in transit (Fig. 2). Fig. 5 is an autoradiograph of 2 vascular bundles of a petiole showing the pattern of silver grains. The highest concentration of silver grains corresponds to the area of the vascular bundle occupied by sieve tubes and companion cells (Fig. 6, 7). A detailed study of the identity of the components of the phloem revealed that the sieve tubes were arranged in groups of 3 to 6 cells surrounded by cambium and parenchyma cells (Fig. 8, 9).

The occurrence of clusters of silver grains

Table IV. *Translocation Rate, Phloem Area and Sieve Tube Area for Petioles of Sugar Beet Plants Used in Translocate Accumulation Study*

Plant	Translocation rate down petiole	Cross sectional area of conduit required to convey translocate[1]	Measured cross sectional area of phloem[2]	Sieve tube cross sectional area[3]	Ratio required area to sieve tube area
	μg C/min	*mm²*	*mm²*		
1	9.3 ± 0.5	0.028	0.103	0.030	0.93
2	7.4 ± 0.5	0.022	0.096	0.028	0.79
3	11.8 ± 0.4	0.035	0.081	0.023	1.52
4	11.8 ± 1.7	0.035	0.075	0.022	1.62
5	12.1 ± 1.1	0.036	0.093	0.027	1.33
6	11.6 ± 0.6	0.035	0.120	0.035	1.00
7	7.6 ± 1.1	0.023	0.070	0.020	1.15
8	...	...	0.208	0.060	...
9	18.9 ± 0.3	0.057	0.123	0.036	1.58
10	19.0 ± 1.1	0.057	0.179	0.052	1.09
11	16.8 ± 1.0	0.051	0.161	0.051	1.00
12	16.1 ± 2.3	0.048	0.122	0.034	1.41
13	13.3 ± 0.7	0.040	0.125	0.039	1.03
M ± SD	10.4 ± 0.1	0.031	0.102	0.023	1.35
					1.21 ± 0.27

[1] Based on a velocity of 0.9 cm/min and a concentration of 8.8 % sucrose in transport stream.
[2] Area of sieve tubes, companion cells, phloem parenchyma exclusive of cap of fiber cells.
[3] An average of 29±3.2 % that was obtained from the plants used for detailed sieve tube measurement (10–14) was used for plants 1 to 9.

Table V. *Cross-Sectional Area of Vascular Bundles in Petiole and Major Veins in 10-cm Leaf of* Beta vulgaris

Vascular structure	Cross-sectional area of entire vascular bundle		Cross-sectional area of phloem			Cross-sectional area of xylem		
	mm²	%	*mm²*	%	%[2]	*mm²*	%	%[2]
Sum of all primary branches of midrib (14 veins contributing to petiole)	1.25	100	0.61	100	49	0.63	100	51
Uppermost zone of petiole (7 vascular bundles)	1.09	87	0.53	90	49	0.56	89	51
Middle zone of petiole (7 vascular bundles)	1.12	90	0.51	84	46	0.61	97	54
Basal zone of petiole (11 vascular bundles)	1.08	86	0.56	92	52	0.52	83	48
Avg		91		91			92	
Primary branch (1 vein)	0.164	100	0.073	100	45	0.091	100	55
Secondary branches which form above branch (2 veins)	0.152	93	0.074	101	49	0.078	86	51
Avg					48.3			51.7

[1] Includes all phloem cell types.
[2] Based on area of entire vascular bundle at a given level.

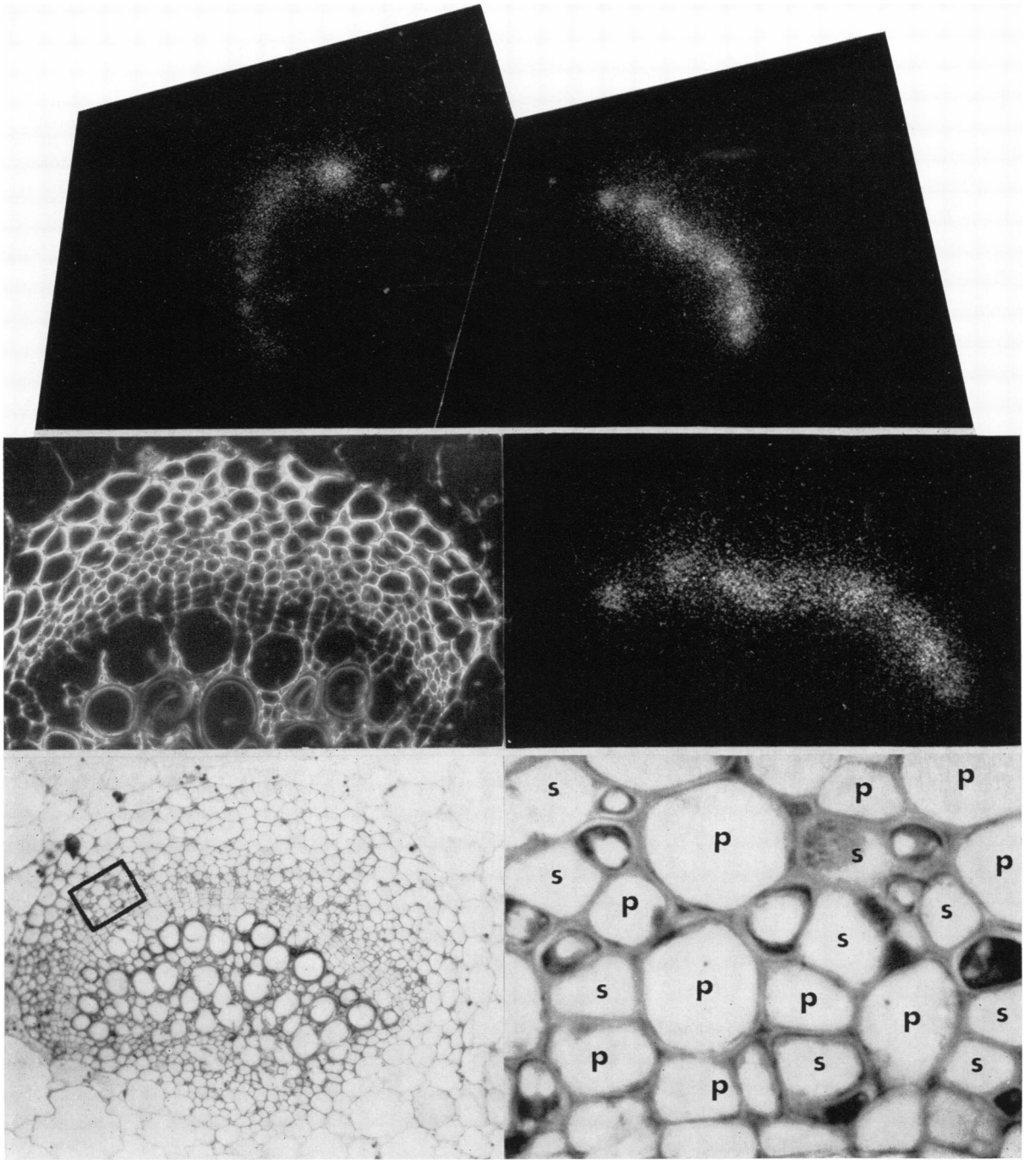


FIG. 5. (Upper) Silver grain pattern from freeze-dry autoradiograph of 2 of 3 vascular boundles in a cross section of a petiole of a 10-cm sugar beet leaf sampled after 60 min of steady state labeling. ×100.

FIGS. 6 and 7. (Middle) Tissue and silver grains from one of the bundles in Fig. 5. ×200.

FIG. 8. (Lower left) Cross section of 1 of 3 vascular bundles in the petiole of plant 13 (in table V). Paraffin section. ×125.

FIG. 9. (Lower right) Detail of sieve tube (s), phloem parenchyma (p) and companion cells (unmarked) from bundle in Fig. 8. ×1,200.

throughout the sieve-tube-containing portion of the phloem is consistent with the conclusion from cross sectional area calculations that nearly all of the sieve tubes were used to convey translocate. Autoradiographs of petiole sections, following 80 %-ethanol extraction, showed a pattern of silver grains which was generally similar to that for sections not extracted. The clusters of higher grain density over the sieve tubes and companion cells were not found. The silver grain pattern indicates that accumulation occurred in regions occupied by sieve tubes, companion cells, phloem parenchyma, cambium and fiber cells. Light microscopy of petiole sections revealed large starch grains in cortex cells immediately adjacent to the phloem while electron micrographs revealed small grains in the plastids of companion and phloem parenchyma cells. Bieleski (1) concluded that primary and secondary phloem, cambium and ray parenchyma cells were most active in accumulation of labeled sulfate and phosphate in isolated phloem tissue while cortical parenchyma and fiber cells showed much less accumulation.

Conclusions

Radiochemical analysis and histoautoradiography both indicate that the petiole is a good, though somewhat variable sink for translocate. Sucrose and 80 %-ethanol insoluble materials constitute important storage forms which presumably buffer fluctuations in the solute concentration of sieve sap during alternating periods of high and low assimilation. Various cells throughout the phloem appear to be sites for this accumulation.

Specific mass transfer values of 1.40 g/hr•cm² phloem or 4.8 g/hr•cm² sieve tube are in good agreement with values previously reported for petioles (2). Calculations of required sieve-tube cross section obtained from mass transfer and velocity measurements indicate that sieve tubes throughout the phloem are required for translocation. Histoautoradiography of phloem, at a time when most of the labeled material is in transit, confirm that most of the sieve tubes are functional.

The correlation ($r = 0.76$) between sieve tube area and mass transfer rate in morphologically similar plants indicates that the cross sectional area of the conducting system limits translocation through the sugar beet petiole. This fact would be consistent with the good agreement between the various specific mass transfer values reported in the literature (2).

Acknowledgment

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