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Sucrose Hydrolysis in Relation to Phloem Translocation in *Beta vulgaris*[1]

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ROBERT GIAQUINTA
Central Research and Development Department,
Experimental Station,
E. I. du Pont de Nemours & Co. Inc., Wilmington, Delaware 19898

ABSTRACT

Asymmetrically labeled sucrose, ^{14}C(fructosyl)sucrose, was used to determine whether sucrose undergoes extracellular hydrolysis during phloem translocation in the sugar beet, *Beta vulgaris*. In addition, the metabolism of various sugars accumulated and translocated was determined in various regions of the plant. These processes were studied in detached regions as well as in the intact, translocating plant in the source leaf, along the translocation path, and in a rapidly growing sink leaf and storage beet. The data show that, unlike sucrose accumulation into the sink tissue of sugarcane, sucrose is neither hydrolzyed prior to phloem loading or during transit, nor is it extracellularly hydrolyzed during accumulation into sink leaves or the storage beet.

Although it is well established that photosynthetically derived assimilates are transported between source and sink regions along a gradient of hydrostatic pressure, relatively little is known about the cellular and metabolic correlates of the translocation process. The translocation system is generally divided into three structurally and physiologically distinct regions: the source, path, and sink regions. Recent structural and physiological studies (5, 10, 17, 18) have indicated that the path region is relatively passive in the translocation process, in that the driving force for transport resides in metabolism-dependent processes operating in the source and sink regions.

From a mechanistic viewpoint, the major emphasis in the phloem transport literature has been toward elucidating the role of the path at the expense of source and sink metabolism, particularly at the cellular level. Recent studies by Geiger and co-workers (12, 13) have investigated events operating in the source leaf of *Beta vulgaris* during the loading of sucrose into the phloem prior to translocation. What has emerged from these studies and from the more recent studies by Giaquinta (14, 15) is that in the source leaf, photosynthetically derived sucrose enters the apoplast at the phloem regions and is then selectively accumulated by an energy-dependent transport process involving phloem membrane sulfhydryl groups. The driving force for sucrose accumulation is possibly coupled to the co-transport of protons generated by phloem membrane ATPase activity (15).

Cellular events associated with the unloading of sugars and their subsequent metabolism in sink regions are less clear. In only one species, sugarcane, has this problem received much attention. It seems clear from the definitive work of Hatch *et al.* (21) that in both immature and mature sugarcane storage sinks, the enzyme invertase plays a central role in the partitioning of assimilates between the processes of sugar storage and growth. Invertase was shown to be localized in the free space where it hydrolyzes translocated sucrose to hexoses which are then actively accumulated into the metabolic compartment and resynthesized back to sucrose. This invertase activity was shown to be the rate-limiting parameter for both sugar uptake and storage in sugarcane tissue (19).

Hydrolysis of sucrose to hexoses by a free space invertase prior to accumulation quite convincingly occurs in sugarcane tissue. The paucity of information on this subject in other species makes it difficult to determine whether these events constitute a general mechanism of sink metabolism of translocate or whether they are characteristic for the sugarcane system.

The literature on the role of extracellular invertase in phloem translocation in both source and sink regions is controversial. Part of the discrepancy and variability probably arises from the observation that invertase activity can be induced in some tissues by physical dissection or prolonged washing (8). Another possibility is that extracellular invertase as related to translocation is not universally present in various species and that sucrose need not be extracellularly hydrolyzed prior to membrane transport into the sink tissue.

The form in which sucrose is transported across cell membranes during phloem translocation is important in elucidating the nature and selectivity of membrane carriers involved in phloem loading and unloading of sugars in the source and sink regions, respectively. In this study, the question of free space sucrose hydrolysis and the subsequent metabolism of the accumulated sugar are investigated in the sugar beet plant, *B. vulgaris*. Specifically, these processes are studied in detached regions as well as in the intact plant in the source leaf, along the translocation path, and in rapidly growing (young leaf) and storage (beet) sink tissues. The results indicate that in the sugar beet plant, sucrose is hydrolyzed neither prior to phloem loading in the source leaf nor extracellularly prior to uptake in a young sink leaf or storage beet.

MATERIALS AND METHODS

B. vulgaris L. (monohybrid A-1) plants were grown in a controlled environment under the following conditions: a 12-hr photoperiod at 3,800 ft-c, 23 C-17 C day-night temperature regime, and 60% relative humidity. Source leaf discs (0.5 cm in diameter) were obtained from interveinal tissue from the upper one-third portion of fully expanded sugar beet leaves of 8- to 10-week-old plants. Discs were also obtained from young sink leaves (3-4 cm in length) in which the lower portion of the leaf lamina was still unrolled. Previous studies (9, 17) have shown that such leaves constitute an exporting source and importing

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sink of assimilates. Tissue from the storage beet was obtained from similar plants which had 40- to 70-g beet. A horizontal bore (0.5 cm in diameter) was made through the upper portion of the white beet (below the Chl-containing crown tissue) since this portion of the beet is most active in sucrose storage. Slices (0.5–1 mm thick) from this cylinder of beet tissue were rinsed in 0.5 mM $CaCl_2$ prior to incubation on ^{14}C-sugars.

The tissues were incubated on various ^{14}C-sugars (New England Nuclear) for 30 min as specified in the table legends. Tissues were washed in several changes of 1 mM $CaCl_2$ or running tap water for 30 to 60 min to remove free space label. The materials were extracted for 6 hr in 80% (v/v) ethanol at 80 C in a Soxhlet extracting apparatus. The alcohol-soluble fraction was passed through coupled cation and anion exchange columns as described previously (16) to obtain the following fractions: (*a*) neutral, mainly sugars eluted with water; (*b*) acidic, eluted with 2 N HCl, containing organic acids and sugar phosphates; and (*c*) basic, mainly amino acids eluted with 2 N NH_4OH. Sugars in the neutral fraction were separated by one-dimensional paper chromatography in 1-butanol-acetic acid-water (3:3:2, v/v/v). The sucrose region was cut from the chromatograms and eluted from the paper by centrifugation (24). The sucrose was enzymically hydrolyzed by incubation in 400 units of yeast invertase (Sigma) containing 100 mM sodium acetate buffer (pH 4.5) at 45 to 50 C for 12 hr. The mixture was reduced in volume and rechromatographed as above to determine the ^{14}C distribution among the hexose moieties. The glucose to fructose ratios (G/F) of the stock ^{14}C(fructosyl)sucrose and ^{14}C(U)sucrose were ≤ 0.01 and 1 ± 0.01, respectively.

The insoluble fraction (precipitated proteins, starch and structural carbohydrates) was digested in a perchloric acid-H_2O_2 mixture as described previously (15). The radioactivity (dpm) was determined by liquid scintillation spectroscopy.

Application of ^{14}C(fructosyl)sucrose to the source leaf of an intact sugar beet plant is described in the text and table legend.

RESULTS AND DISCUSSION

In a series of papers by Hatch *et al.* (21), asymmetrically labeled sucrose was employed to show that sucrose was hydrolyzed prior to membrane transport into immature sugarcane stalks. Similarly, Hawker and Hatch (22) used the same technique to show sucrose inversion during uptake in mature sugarcane storage stalks. On the other hand, Kriedemann and Beevers (24), using ^{14}C(fructosyl)sucrose showed that sucrose was not hydrolyzed prior to uptake into castor bean cotyledons.

The rationale of this methodology is that if the asymmetrically labeled sucrose is hydrolyzed by extracellular invertase prior to uptake and the hexoses then resynthesized to sucrose once in the symplasm, the resynthesis process would, because of isomerase activity, introduce randomization of the radiocarbon among the hexose moieties of the sucrose molecule. Maintenance of the asymmetry of the ^{14}C in the sucrose molecule after accumulation is evidence for sucrose entering the metabolic space intact, without hydrolysis. This technique along with determining the distribution of ^{14}C into various metabolite fractions was used to study sucrose uptake into source and sink leaves and the storage root of the sugar beet plant.

Source Leaf. It has been established that sucrose enters the apoplast prior to accumulation into the phloem in source leaves of the sugar beet plant (12–14). Brovchenko (2) concluded that sucrose is hydrolyzed by a free space invertase prior to phloem loading in the source leaf. This work has been criticized because it involved physical dissection and prolonged washing (24 hr) of the tissue prior to experimentation. These procedures have been shown to induce invertase activity (8). Others workers contend that sucrose is accumulated *per se* by a sucrose-specific carrier mechanism in the phloem membranes (11, 15). To distinguish between these alternatives, the accumulation of ^{14}C-(fructosyl)sucrose was determined in sugar beet source leaves. Table I shows the ^{14}C-metabolite distribution pattern in source leaf tissue after a 30-min accumulation period on various ^{14}C-sugars. When either uniformly or asymmetrically labeled sucrose was accumulated, 90% of the radiocarbon was incorporated into water-soluble materials with sucrose being the major species labeled. There was little evidence for extensive metabolism of the sugar into the basic, acidic, insoluble, and hexose fractions. This is in agreement with our previous data (15) which demonstrated by autoradiography and metabolite distribution that the sucrose entering source leaves accumulated in the minor veins of the phloem and not the mesophyll cells. In contrast to sucrose, ^{14}C-glucose is preferentially accumulated into the mesophyll (3) and metabolized into various components, showing a 3-fold increase of ^{14}C incorporation into the insoluble fraction (30%) along with the nearly equal distribution of label among the netural (37%), acid (34%), and basic (28%) fractions. Autoradiographs of source leaf tissue incubated in ^{14}C-glucose showed extensive mesophyll labeling (15) in contrast to minor vein accumulation, consistent with mesophyll uptake and metabolism.

Importantly, when ^{14}C(fructosyl)sucrose is accumulated into the source, the glucose to fructose ratio of the accumulated sucrose was 0.02 (Table I), indicating very little randomization of the label (about 2%) among the hexose moieties. When uniformly labeled sucrose was accumulated, the G/F ratio was essentially 1, as expected. That the tissue contained active isomerase activity, so that ^{14}C randomization would have resulted if hydrolysis and resynthesis occurred, is indicated by that data showing that when ^{14}C-glucose is accumulated, the resulting synthesized sucrose has a G/F ratio of unity, indicating complete randomization between the hexoses. These results and autoradiographic data presented earlier (15) indicate that sucrose accumulated from the free space enters the phloem and is accumulated without free space hydrolysis by a sucrose-specific carrier.

Sink Leaf. In contrast to the source leaf, when young sink leaf tissue is incubated in either uniformly or asymmetrically labeled sucrose, a substantial amount of ^{14}C enters the insoluble fraction (approximately 40%) which is comprised of protein, starch, and structural components (Table II). The distribution pattern following sucrose uptake into sink leaf tissue closely resembles that found after glucose uptake into source tissue (evidently both processes reflect mesophyll uptake and metabolism) in that the label is nearly equally distributed among the basic, acidic, and neutral fractions (30–40%). This is consistent with the autoradiographic results of Fellows and Geiger (9) which showed that in sugar beet sink leaf tissue incubated on sucrose, label was localized mainly in the mesophyll cells and not in the phloem. When ^{14}C-glucose is accumulated by the sink leaves, a distribution pattern similar to that following sucrose uptake is obtained

TABLE I. Metabolite distribution following accumulation of ^{14}C-sugars in source leaf tissue of Beta vulgaris

Fraction	Sugar Supplied		
	^{14}C(U)sucrose	^{14}C(fructosyl)sucrose (%)	^{14}C(U)glucose
Insoluble	10	8	30
Water Soluble	90	92	70
Basic	10	5	28
Acidic	10	3	34
Neutral	80	92	37
Glucose	10	2	23
Fructose	5	8	15
Sucrose	85	90	62
G/F	0.99	0.02	1.0

Ten discs of source leaf tissue were incubated in 5 mM ^{14}C-sugar (3μCi/μmole) for 30 min. G/F ratio represents the glucose to fructose ratio obtained from sucrose after invertase treatment.

(Table II). This is unlike source leaf accumulation which showed marked differences in the metabolism of ^{14}C-sucrose and ^{14}C-glucose (Table I), reflecting differences in metabolism and/or compartmentalization in source and sink leaf tissue. These results indicate that the sucrose transported to sink leaf tissue is rapidly metabolized into various metabolites. This is a reasonable conclusion since a young growing leaf requires assimilates for metabolism and energy for a variety of growth processes including respiration, and protein and cell wall biosynthesis. What is important, however, from a mechanistic viewpoint, is whether the translocated sucrose is hydrolyzed *extra*cellularly prior to mesophyll uptake or whether the sucrose is accumulated intact and then hydrolyzed *intra*cellularly for subsequent metabolism by an invertase or sucrose synthetase in the symplasm. The G/F ratio of 0.02 after accumulation of ^{14}C(fructosyl)sucrose indicates the latter. Even though the neutral fraction only represents 30% of the ^{14}C in the water-soluble fraction, the labeled sucrose in this fraction seems to represent sucrose which was accumulated without hydrolysis and not metabolized until needed. In a resynthesized sucrose pool randomization of the label would have occurred as shown by the G/F ratio of 0.78 when ^{14}C-fructose was accumulated (Table II). As a control, uniformly labeled sucrose gave the expected G/F ratio of unity. These data also indicate that sink leaf tissue can accumulate both sucrose and glucose and that the rates of uptake are nearly equal for both sugars, about 40 nmol/hr·mg dry wt.

Storage Beet. As mentioned in the introductory section, most of the research on sink metabolism has been directed toward the mechanisms involved in sucrose storage in stalks of sugarcane (19). Experiments conducted on both immature and mature sugarcane stalk revealed significant randomization of the ^{14}C label after accumulation of asymmetrically labeled sucrose into these tissues. The relatively sparse data on the sugar beet storage root are less definitive. The Russian workers (1, 7, 8), who did not employ asymmetrically labeled sucrose to study this uptake, have reported conflicting results on the question of sucrose hydrolysis, showing the presence or absence of invertase depending on the region of the root sampled, the age or nutrition of the beet, or whether tissue cultured materials were used.

Sucrose hydrolysis in the sugar beet root is particularly interesting in that it can be directly compared to the sugarcane stalk because both organs are active sucrose-storing sinks. Also, since the sugarcane system has been studied in detail there are ample data for direct comparison.

Table III shows the metabolite distribution of ^{14}C label along with the glucose to fructose ratio of the accumulated sucrose in the sugar beet storage root following accumulation of various ^{14}C-sugars. After a 30-min incubation period in either ^{14}C(U)sucrose or ^{14}C(fructosyl)sucrose, essentially all of the label is present in the sucrose fraction (storage) with little evidence of the accumulated sucrose being further metabolized. As in the case of source and sink leaves, when ^{14}C-labeled hexoses were accumulated in beet tissue more of the ^{14}C appeared in the insoluble, basic, and acidic fractions indicating the metabolic as well as the storage capacity of the beet. Sucrose can be synthesized from labeled hexoses, indicating sucrose-synthesizing capability of the storage root. This ability may be necessary for the partitioning of carbon between storage compartments and metabolism needed for root maintenance and growth. The rate of hexose uptake into beet tissue was about equal to that of sucrose uptake, namely 21.6, 21, and 22 nmol/hr·disc for ^{14}C-glucose, ^{14}C-fructose, and ^{14}C(U)sucrose, respectively.

TABLE II. Metabolite distribution following accumulation of ^{14}C-sugars in sink leaf tissue of Beta vulgaris

Fraction	Sugar Supplied			
	^{14}C(U)sucrose	^{14}C(fructosyl)sucrose	^{14}C(U)glucose	^{14}C(U)fructose
	(%)			
Insoluble	43	42	37	47
Water soluble	57	57	63	53
Basic	28	38	33	22
Acidic	28	35	36	40
Neutral	44	27	33	38
Glucose	23	10	51	10
Fructose	17	5	15	51
Sucrose	60	85	34	39
G/F	1.0	0.02	-	0.78

Ten discs of sink leaf tissue were incubated in 5 mM ^{14}C-sugar (4μCi/μmole) for 30 min prior to extraction.

TABLE III. Metabolite distribution following accumulation of ^{14}C-sugars in the storage beet of Beta vulgaris

Fraction	Sugar Supplied			
	^{14}C(U)sucrose	^{14}C(fructosyl)sucrose	^{14}C(U)glucose	^{14}C(U)fructose
	(%)			
Insoluble	3	3	21	18
Water Soluble	97	97	79	82
Basic	1	1	9	7
Acidic	6	3	35	44
Neutral	93	97	57	49
Glucose	2	1	37	5
Fructose	1	1	5	34
Sucrose	97	98	57	62
G/F	1	0.007	1.2	0.7

Ten discs each of beet tissue (as described in Materials and Methods) were incubated in 5 mM ^{14}C-sugar (9μCi/μmole) for 30 min and then washed for 30 to 45 min in 1 mM $CaCl_2$ prior to extraction.

The glucose to fructose ratios of sucrose accumulated from the various sugars show that there is very little randomization of the label (less than 1%) when ^{14}C(fructosyl)sucrose is offered. The sucrose synthesized from labeled glucose and fructose has a G/F ratio of 1.2 and 0.7, respectively, indicating substantial randomization due to isomerization between the hexoses. As a control uniformly labeled sucrose gave the predicted value of unity. These results demonstrate that sucrose hydrolysis does not occur prior or subsequent to accumulation (at least under short term conditions) in the sugar beet storage root.

To test the reliability of our procedures we reexamined sucrose uptake into sugarcane stalk tissue, a system which necessitates sucrose hydrolysis prior to uptake. Table IV shows the metabolite distribution pattern after accumulation of ^{14}C-(fructosyl)sucrose into immature and mature sugarcane stalk tissue. As with the growing sink leaf of sugar beet, the immature sugarcane stalk tissue incorporated more ^{14}C label into the insoluble fraction (24%) than did the mature tissue (<1%). More label was also found in the basic and acid fractions in the immature compared to mature tissue. Notwithstanding, sucrose is still the major metabolite labeled in both tissues. Importantly, the glucose to fructose ratio of the sucrose in both tissues is approximately 0.25, a value close to the ratio of 0.3 reported for sugarcane tissue (21) indicating extracellular sucrose hydrolysis.

Intact Plant. Table V shows the G/F ratio of sucrose extracted from various regions of an intact sugar beet plant after feeding the source leaf ^{14}C(fructosyl)sucrose for 6 hr. A G/F ratio of $\leq$0.05 was obtained from all portions of the translocation system indicating lack of substantial sucrose hydrolysis during translocation. Hatch and Glasziou (20) conducted a similar experiment with the sugarcane plant. The sucrose from the source and path regions in sugarcane had a G/F of $\leq$0.05 while internal parenchyma sink tissue gave a G/F ratio of 0.1 to 0.2, consistent with their previous results (21) showing sucrose hydrolysis in the free space of sink tissue.

TABLE IV. Metabolite distribution and glucose/fructose ratio after accumulation of ^{14}C(fructosyl)sucrose into immature and mature sugarcane stalk tissues

Fraction	Immature	Mature
	(%)	
Insoluble	24	0.2
Water soluble	76	100
Basic	4	0.2
Acidic	7	2
Neutral	89	98
Glucose	3	4
Fructose	7	1
Sucrose	90	95
G/F	0.25	0.2-0.25

Several discs from immature and mature stalks of sugarcane were incubated in 10 mM ^{14}C(fructosyl) sucrose for 30 min, washed for 60 min and extracted.

TABLE V. Glucose/Fructose ratio of sucrose after accumulation of ^{14}C(fructosyl)sucrose in various plant regions after translocation in the intact sugar beet plant

Plant Region	G/F Ratio of Sucrose
Source Leaf Lamina	0.02-0.05[1]
Source Leaf Midrib	0.04
Source Leaf Petiole	$\leq$0.05
Sink leaf Lamina	$\leq$0.05
Storage Beet	$\leq$0.05

^{14}C(fructosyl)sucrose at 10 mM was applied to an abraded area of source leaf in a sugar beet plant trimmed to a source-path-sink system (12). After 6 hr various regions were excised, frozen in solid CO_2 and extracted according to procedures given in Materials and Methods.

[1]Extracted 30 min after ^{14}C(F)sucrose application.

The data presented here for the sugar beet plant indicate that sucrose *per se* is selectively accumulated into the phloem in the source leaf, is translocated without significant hydrolysis along the path (source leaf midrib and petiole), and enters the metabolic and storage spaces of young leaves and the beet, respectively, without extracellular hydrolysis. Once in the metabolic space of the sink leaf, sucrose is readily metabolized for various growth and biosynthetic processes. It thus appears that the mechanisms operating in sugar storage in the sugar beet and sugarcane plant are different.

A survey of the literature indicates that sucrose can be accumulated without free space hydrolysis in a variety of plant regions that would have to be considered translocation sinks. Jenner (23) has recently shown that extracellular hydrolysis of sucrose did not occur prior to uptake of sucrose in wheat grains. Similarly, young pea (6) and tomato roots (4) as well as bean pod tissue (25) are capable of absorbing sucrose without prior hydrolysis. Thus, sucrose hydrolysis in the apoplast does not seem to be a universal feature of sink tissue metabolism in terms of the translocation process.

According to the data presented here, sucrose *per se* enters the source leaf phloem, sink leaf mesophyll and storage beet parenchyma without extracellular hydrolysis. Although it is well established that sucrose is accumulated into the phloem from the apoplast in the source leaf (12, 14) there is no information available on the transport pathway in sink regions. Thus the data for sink leaf and storage beet are consistent with either an apoplastic or symplastic route of *sucrose* into these regions.

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