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Sucrose Uptake by Sugar Beet Tap Root Tissue[1]

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ABSTRACT

Sucrose uptake by discs of mature sugar beet root tissue incubated in [^{14}C]-sucrose exhibited nonsaturating kinetics over the concentration range of 1 to 500 millimolar. Uptake was inhibited by dinitrophenol, sodium cyanide, low O_2, and penetrating sulfhydryl inhibitors. ATPase inhibitors, sodium fluoride, and oligomycin reduced uptake by 20 and 40%, respectively. Uptake as asymmetrically labeled sucrose ([^{14}C]glucose) occurred with approximately 80% retention of asymmetry, indicating a nonhydrolytic pathway. Uptake was against a concentration gradient and required metabolic energy.

Glucose and fructose uptake exhibited typical saturation kinetics but rates of uptake were lower than that of sucrose, particularly at high concentration. Glucose strongly inhibited the uptake of sucrose and fructose but sucrose and fructose had little effect on the rate of glucose uptake. It is proposed that a major portion of the sucrose movement between its free space and vacuole occurs via a nonsaturating carrier at sites where the plasmalemma and tonoplast are appressed.

Two important aspects of a plant's productivity are: (*a*) its capacity to produce large amounts of photosynthates; and (*b*) its ability to transport and partition these photosynthates to appropriate sink areas. Of particular importance to food production is the ability of agronomic plants to partition a large proportion of assimilate to the economically important sink, *i.e.* the grain, tuber, root, or foliage. Major research emphasis has been placed on photosynthesis and transport of assimilate, but relatively little information is available on the effect of the sink region on partitioning and thus agronomic productivity. An important aspect of sink metabolism is the capacity of the sink to assimilate translocated sucrose.

The mechanism of phloem unloading and subsequent uptake of sucrose by cells within the sink region is not well understood. Only in sugarcane is the uptake of sucrose from the free space and its subsequent storage in the vacuole well understood (for review see ref. 9). In sugarcane, sucrose is hydrolyzed before uptake into the metabolic compartment (18); in developing corn kernels, sucrose is hydrolyzed before movement into the developing endosperm (19). This hydrolysis of sucrose does not appear to be a universal requirement in plants.

Sucrose uptake without prior hydrolysis has been demonstrated in developing wheat grains (11), pea roots (5), tomato roots (3), bean pod tissue (17), in castor bean seedlings (13), and recently in sugar beet (8). There is evidence that sucrose translocated into sugar beet root is unloaded into the free space (21; Wyse, in preparation), however, the mechanism of its uptake into the storage vacuole is not known.

In this investigation I studied the mechanism of sucrose movement from the free space into the vacuoles of storage parenchyma cells. The results confirm the observation that a major portion of the sucrose taken up from the free space and stored in the vacuole of sugar beet tap root cells is not hydrolyzed and indicate that membrane transport is via a nonsaturating carrier. I propose that the carrier is located in regions where the plasmalemma and tonoplast are closely appressed, thus allowing sucrose uptake without direct contact with the cytoplasm.

MATERIALS AND METHODS

Tap roots of *Beta vulgaris* L. (cultivar Mono Hy-D2) plants grown either in the greenhouse or the field were used. Greenhouse plants were grown under the following conditions: 16-h photoperiod (daylight hours were extended using incandescent and Gro-Lux[2] fluorescent lighting); approximately a 25 C/18 C, day/night temperature cycle; 10-liter pots with a 1:1:1 peat moss-Vermiculite-sand mix. The plants were fertilized weekly with a complete nutrient solution. Field-grown plants had consistently higher rates of sucrose uptake than greenhouse-grown plants, but no significant differences were observed in the characteristics of uptake. All plants utilized were 3 to 6 months old with root weights of 0.4 to 1.5 kg and sucrose contents of 13 to 16% fresh weight.

Discs of root tissue, normally from a single root, were prepared by cutting 1.0-mm-thick slices with a hand-microtome. Discs 5 mm in diameter were then cut from these slices with a cork borer. The discs were washed for 30 min in running tap water before incubation with labeled sugars. Twenty discs were placed in a vial containing labeled sugars and 1 ml of 5 mM phosphate buffer (pH 6.5). During the incubation period, humidifed air was bubbled through each vial to prevent anaerobiosis. After incubation for 3 h, the discs were again washed in running tap water for 30 min to remove labeled sugars in the free space. After washing, the discs were placed in liquid scintillation vials containing 10 ml of hot 80% ethanol, heated to boiling for 30 min, capped, and allowed to stand overnight at 5 C. Ethanol was removed by boiling and the residue was dissolved in 2 ml of distilled H_2O. Radioactivity was determined by liquid scintillation spectroscopy. All rates of uptake are expressed as μmol/3 h·20 discs. Twenty discs weigh about 0.5 g fresh weight.

The possible interconversion of sugars during uptake was studied. After incubation and a 30-min tap water wash, root discs were extracted for 2 h with 80% ethanol in a Soxhlet apparatus. The extract was concentrated under vacuum at 35 C and deionized on coupled anion (AG 1-X8) and cation (AG 50W-X8) columns. The deionized extract was evaporated to dryness under vacuum at 35 C and reconstituted in a minimal amount of water. Separation of

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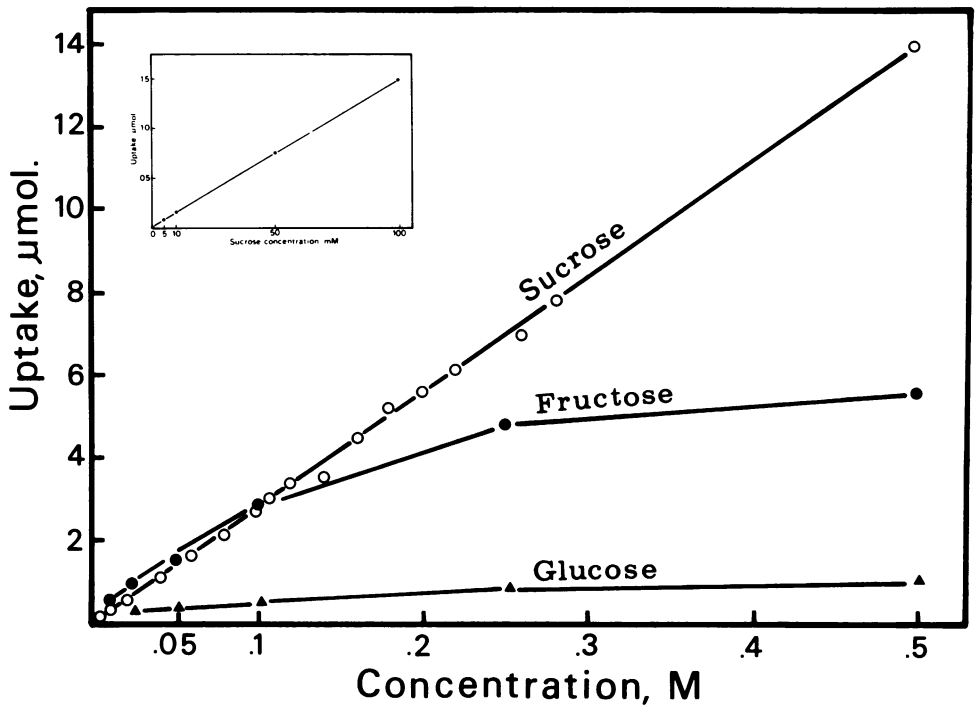

FIG. 1. Relationship between concentration and rate of uptake of sucrose, glucose, and fructose by sugar beet root tissue. Discs of root tissue were incubated for 3 h.

the major sugars (glucose, fructose, and sucrose) was by a two-step sequence on a Whatman Partisil-10 PAC column using a Spectra Physics HPLC system, with a Waters refractive index detector. The samples were first separated into mono- and disaccharide fractions using a preparative column (9.6 mm × 25 cm) with acetonitrile-2.5 mM acetate (pH 5.0) buffer (86:14) solvent. The occluded glucose and fructose peaks were concentrated and separated using the same solvent but in a 94:6 ratio on an analytical Partisil-10 PAC column (4.6 mm × 25 cm). The separated peaks of interest were collected, evaporated to dryness at 80 C, redissolved in 2 ml of water, and radioactivity was determined using liquid scintillation techniques.

RESULTS AND DISCUSSION

Characteristics of Sucrose Uptake. Sucrose uptake from a 0.05 M sucrose solution was linear over a 3-h period. All kinetic experiments reported here did not exceed this time interval.

Sucrose uptake was also linear over the concentration range of 0.5 to 500 mM (Fig. 1). The curve showed no biphasic nature as found previously in sugar beet leaf discs (20). Adjusting the incubation media to isotonicity (0.67 M) with mannitol did not affect the linearity or rate of uptake.

The sucrose concentration of mature sugar beet roots may be as high as 20% of the fresh weight (75% of the dry weight). The sucrose content of the tissues used in these experiments ranged from 13 to 16% fresh weight. If one assumes this sucrose to be uniformly distributed in the cell water, the molar sucrose concentration in these roots was a minimum of 0.5 to 0.6 M. Uptake over the concentration range shown in Figure 1 was against a concentration gradient. This experiment has been repeated many times and in no case was saturation kinetics observed for sucrose uptake. These data suggest that either the rate-limiting step is one of diffusion, or that the transfer system is totally responsive to concentrations of sucrose in the free space as high as 0.5 M.

In contrast to the linear uptake of sucrose, both glucose and fructose exhibited saturation kinetics. The rate of glucose uptake was extremely slow (approximately 1 µmol/3 h·20 discs). The faster rate of sucrose uptake compared to the hexose sugars would support evidence that sucrose is not hydrolyzed before storage in the vacuole (8). If mandatory hydrolysis occurred, one could logically deduce that the uptake of glucose and fructose would be faster than that of sucrose.

The uptake of sucrose was at maximum in a bathing medium at equilibrium with air containing in excess of 21% O_2. Below 21% O_2, the rate of uptake was reduced by as much as 70% at 0% O_2 (Fig. 2). Cyanide (5 mM) reduced uptake to near zero over a sucrose concentration range of 0.1 to 0.5 M. If diffusion were occurring at the high sucrose concentration (0.5 M), uptake in NaCN should show a concave upward response. The uptake in NaCN was low and linear, indicating that the diffusion factor was of minor importance. Temperature studies and use of metabolic inhibitors also indicated that sucrose uptake was active.

Uptake was also inhibited 57% by 3 mM DNP[3] indicating a dependence on oxidative phosphorylation (Table I). Reducing the incubation temperature from 25 to 5 C reduced uptake by 67%. Sodium fluoride had very little effect on sucrose uptake, suggesting that ATPase or acid phosphatase activity is not essential to uptake. NEM, a penetrating sulfhydryl inhibitor, caused a 93% decrease in uptake but the nonpenetrating, sulfhydryl inhibitor, PCMBSA, had little effect. TNBS, a nonpenetrating amino-reactive inhibitor, strongly inhibited uptake, suggesting participation of an amino group. Oligomycin significantly reduced uptake. Inhibition by DNP and oligomycin supports oxidative phosphorylation as a required energy source for sucrose uptake. The lack of inhibition by NaF indicates that ATPase activity is probably not involved.

Lack of inhibition by the nonpenetrating inhibitor PCMBSA indicates that the rate-limiting mechanism is either not accessible on the plasmalemma or occurs at the tonoplast where PCMBSA is not able to penetrate. Although TNBS is normally not a penetrating inhibitor, the long exposure time (2 h) may have allowed uptake after general membrane perturbation. The ability of the metabolic inhibitors and low temperature to inhibit sucrose

[3] Abbreviations: DNP: 2,4-dinitrophenol; NEM: *N*-ethylmaleimide; PCMBSA: *p*-chloromercuribenzene sulfonic acid; TNBS: 2,4,6-trinitrobenzene sulfonic acid.

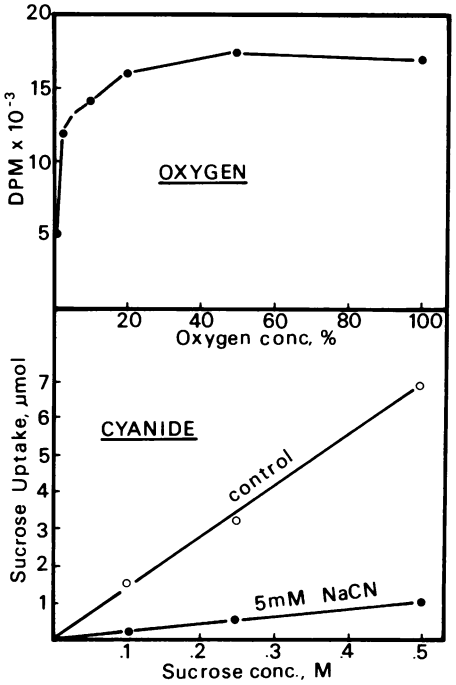

FIG. 2. Effect of O_2 concentration and 5 mM NaCN on sucrose uptake by sugar beet root tissue. A continuous supply of each O_2 concentration was prepared by dilution of air or O_2 with N_2 using flow meters. O_2 concentrations were monitored by gas chromatography. Sucrose concentrations in O_2 experiment was 0.2 M.

Table I. *Effect of Temperature and Selected Inhibitors on Sucrose Uptake by Sugar Beet Root Tissue*

Sucrose concentration in the incubation medium was 0.1 M (specific radioactivity 12,500 dpm/μmol). The rate of uptake by the control was 1.5 μmol/3 h·20 discs.

Treatment	Inhibition
	%
Control, 25 C	0
5 C	67
DNP, 3 mM	57
NaF, 10 mM	9
Oligomycin, 10 μg/ml	37
TNBS, 5 mM	71
NEM, 5 mM	93
PCMBSA, 2.5 mM	13

uptake indicates that the linear uptake of sucrose with increased concentration is a result of a preponderance of active uptake rather than a solely diffusion-limited process.

Effect of pH. Citrate-phosphate buffer (10 mM) was used to control the pH of the incubation media. The uptake of sucrose by root discs decreased only slightly over the pH range 4.2 to 7.5 in the presence of 0.1 M sucrose. Glucose and fructose uptake rates showed weak maxima near pH 5.2 (Fig. 3).

Competition between Sugars. Uptake of sucrose from a 0.2 M solution was inhibited 83% by 1 mM glucose and was essentially stopped by 25 mM glucose. Fructose showed nonspecific inhibition up to 0.1 M (Fig. 4).

Glucose inhibition was linear over a range of sucrose concentrations from 0.05 to 0.5 M (Fig. 5). Attempts to determine if glucose inhibition was competitive were unsuccessful due to nonsaturating characteristics and high concentrations of sucrose required to obtain meaningful Lineweaver-Burk plots.

Glucose and fructose inhibited sucrose uptake, but sucrose had little effect on the uptake of glucose and fructose (Table II). Glucose also strongly inhibited fructose uptake, but fructose had no effect on glucose. These data suggest that each sugar is taken up by a different "carrier" but that glucose may have regulatory capacities on the uptake of fructose and sucrose.

Uptake of sucrose in the presence of glucose and 3-*O*-methylglucose was inhibited approximately 70% (Table III). Preincubation of the tissue in glucose followed by removal of glucose in the free space by washing had no effect on the subsequent uptake of sucrose. Preincubation in 3-*O*-methylglucose inhibited sucrose uptake by 15%. About 25% of the 3-*O*-methylglucose taken up by the tissue was converted to other compounds. The remainder was stored as 3-*O*-methylglucose, presumably in the vacuole. The results indicate that glucose inhibition is reversible and that glucose must be present in the free space to inhibit sucrose uptake.

Asymmetrical Sucrose Uptake. The extent of sucrose hydrolysis during movement from the free space into the vacuole was determined using asymmetrically labeled sucrose [sucrose ([^{14}C]glucose). Sucrose retained in the free space showed little evidence of sucrose hydrolysis and resynthesis as indicated by the retention of 98% of the label in the glucose moiety (Table IV). Sucrose extracted from the vacuole contained 70% of its counts in the

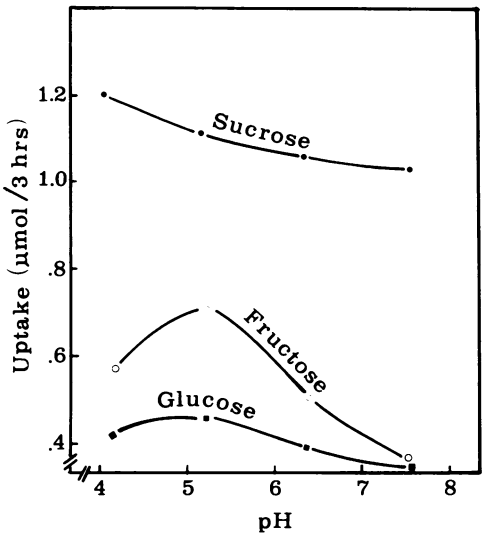

FIG. 3. Effect of pH on uptake of sucrose (●), glucose (■), and fructose (○) by sugar beet root tissue. Root discs were incubated in 20 mM citrate-phosphate buffer containing 0.1 M ^{14}C-sugar (specific radioactivity 4,000 dpm/μmol).

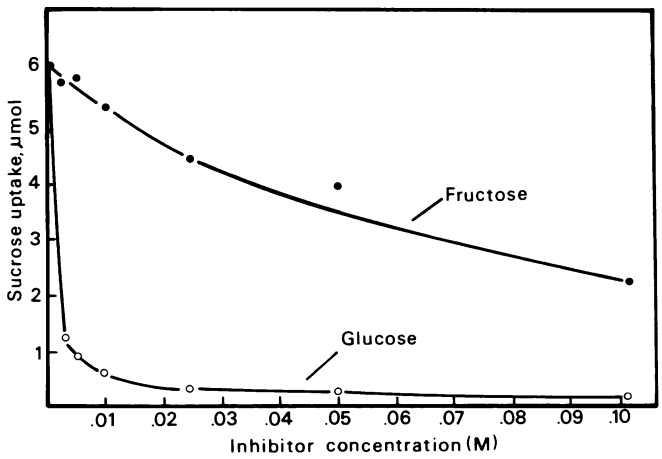

FIG. 4. Inhibition of sucrose uptake by glucose and fructose. Sucrose concentration in the incubation medium was 0.1 M.

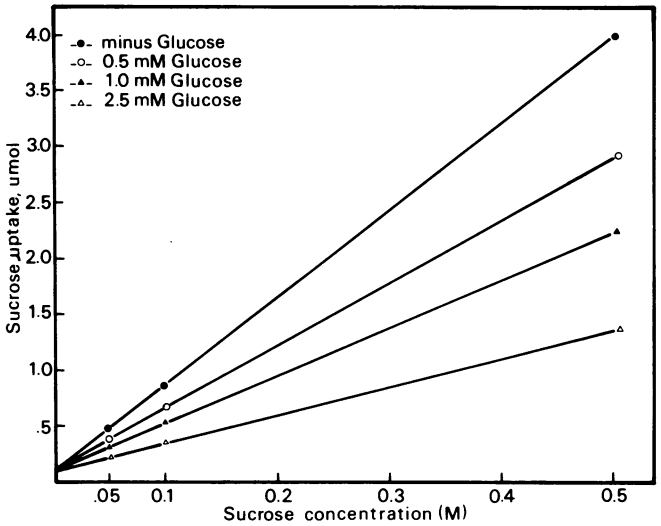

FIG. 5. Effect of low levels of glucose on sucrose uptake.

Table II. *Reciprocal Inhibition of Sucrose, Glucose, and Fructose during Their Uptake by Sugar Beet Root Tissue*

Discs were incubated as described previously. The labeled uptake sugar was 0.1 M and the competing sugar 0.05 M.

Uptake Sugar	Uptake	Inhibitor		
		Sucrose	Glucose	Fructose
	μmol		*% inhibition*	
Sucrose	2.35		81.3	59.4
Glucose	0.3	7.8		2.6
Fructose	1.07	2.6	74.1	

Table III. *Inhibition of Sucrose Uptake by Glucose or 3-O-Methylglucose*

Tissue discs were preincubated for 1 h with aeration and washed for 30 min in running tap water before incubation in 0.1 M sucrose (specific radioactivity 1.82×10^4 dpm/μmol) for 3 h. After incubation the discs were washed for 30 min before hot ethanol extraction.

Preincubation Medium	Incubation Medium	Uptake	Inhibition
		μmol	*%*
Water	0.1 M Sucrose	0.59	0
Water	0.1 M Sucrose 0.01 M Glucose	0.17	71
Water	0.1 M Sucrose 0.01 M 3-methyl-D-Glucose	0.15	74
0.01 M Glucose	0.1 M Sucrose	0.60	0
0.01 M 3-O-Methylglucose	0.1 M Sucrose	0.50	15

glucose moiety and 30% in fructose, indicating partial hydrolysis and resynthesis during uptake.

Complete retention of asymmetry would indicate no hydrolysis during uptake, and thus, no interaction with the hexose pools within the cytoplasm. Loss of asymmetry indicates hydrolysis and interaction with hexose pools within the cytoplasm. An accurate estimate of the proportion of sucrose hydrolyzed cannot be determined from the G/F ratio of sucrose extracted from the vacuole. For example, if hydrolysis occurred and fructose were converted to glucose by P-glucoisomerase, the accuracy of estimating the extent of hydrolysis would depend on the relative rates of turnover of glucose and fructose before the resynthesis of sucrose. If glucose turnover were rapid, the estimate of sucrose hydrolysis would be too low. Therefore, these results indicate some degree of hydrolysis but also indicate that a major portion of the sucrose moving from the free space to the vacuole does so without prior hydrolysis.

Giaquinta (8) found no evidence of sucrose hydrolysis during its movement from the free space into the storage vacuole of sugar beet root tissue. The data in this study showed an estimated 20 to 30% hydrolysis. The difference may be explained in the much longer incubation period used in this study, thus allowing time for interconversions before uptake into the vacuole. Although a high proportion of the sucrose is not hydrolyzed, about 10% of the ^{14}C-labeled sucrose taken up can be detected as $^{14}CO_2$ released by respiration (unpublished data). We also have evidence for sucrose incorporation into starch (Wyse *et al.*, manuscript in preparation). Therefore, sucrose is metabolized in the cytoplasm and a portion may be resynthesized prior to storage in the vacuole.

Table IV. *Distribution of Label in Sucrose after Uptake of Asymmetrical Sucrose ([^{14}C]Glucose)*

After incubation in 0.2 sucrose (specific radioactivity sucrose ([^{14}C]-glucose) 1385 dpm/μmol) for 3 h discs were rinsed for 30 s and then washed for 30 min in distilled H_2O. The water-extracted discs were then extracted with 80% ethanol.

Fraction	Glucose	Fructose
	% composition	
Incubation medium	100	0
30-min wash	98	2
Ethanol extract	76	24

The uptake of sucrose without prior hydrolysis in other plant tissues has shown saturation kinetics (13, 17, 24). Saturation kinetics strongly imply uptake by a carrier system with specific binding sites, whereas nonsaturating kinetics imply a diffusion-limited system. The data presented argue against a major role for a diffusion mechanism in sugar beet root tissue. First, sucrose uptake was highly dependent on metabolic energy, even at relatively high external concentrations. Second, uptake was against a concentration gradient. Third, uptake was strongly inhibited by glucose. It is possible that the carrier systems involved are saturated only at very high nonphysiological concentrations. Nonsaturating mechanisms have been observed for amino acids (4) and for ions (7, 23). The low affinity ion uptake mechanism apparently does not saturate and cannot be explained by diffusion.

The data do not eliminate the possible passive movement of sucrose across the plasmalemma with an active concentrating step at the tonoplast. The 30-min wash after incubation would allow a considerable amount of sucrose to remain in the cytoplasm. If the plasmalemma were leaky, the amount of sucrose in the cytoplasm would exhibit nonsaturation kinetics and would mask saturation kinetics at the tonoplast. Previous work by Parr and Edelman (16) showed that the plasmalemma in carrot callus tissue was relatively permeable to sucrose. A recent report by Doll *et al.* (6) indicates active transport at the tonoplast in isolated vacuoles from red beet.

Pinocytosis has been proposed as a possible mechanism to explain nonsaturation kinetics for ion uptake in the plant tissue (2, 15, 22). A pinocytotic mechanism of sucrose uptake would explain the nonsaturating kinetics, specificity, lack of hydrolysis, and the energy-requiring characteristics observed in this study (1). However, if pinocytosis were operative, some nonspecific uptake would occur in the void volume of the pinocytotic vesicles. Glucose and fructose showed no nonspecific characteristics at high external concentrations, thus making the the pinocytotic mechanism doubtful.

Parenchyma cells in the sugar beet root, particularly those near the vascular bundles, contain numerous invaginations of the plasmalemma membrane. These invaginations put the plasmalemma and tonoplast immediately adjacent to each other (Wyse *et al.*, in preparation). These sites would provide a physical means by which sucrose could be transported from the free space to the vacuole and thus bypass the cytoplasm. Although no direct evidence is available to substantiate a cytoplasmic bypass, the uptake of a major portion of sucrose without prior hydrolysis would

suggest such a pathway. The sugar beet root contains high levels of soluble sucrose synthetase activity (25); thus, any sucrose transported through the cytoplasm would likely be broken down by this enzyme unless the sucrose moving through the cytoplasm and into the vacuole were highly compartmentalized.

The interaction among sucrose, glucose, and fructose during uptake suggests an independent mechanism for each sugar. I am not aware of previous reports of glucose inhibition of sucrose uptake in tissue where sucrose is not hydrolyzed before or during uptake. Glucose is a strong inhibitor of fructose uptake into the vascular tissue of sugar beet petioles, but fructose had little effect on glucose uptake (14). This interaction was explained by the activity of a nonspecific hexokinase. A similar observation was made by Grant and Beevers (10) in corn and carrot tissues. They found that glucose inhibited the uptake of hexose sugars, but neither fructose, galactose, mannose, ribose, sucrose, lactose, nor maltose has any effect on glucose uptake.

Sucrose uptake into sugar beet root tissue was essentially independent of pH. This is in contrast to sucrose accumulation into source leaf tissue which has a pH optimum of 5 to 6 in the external medium (8). Uptake into castor bean cotyledons showed no effect of pH between pH 5 and 8 (12). Since sucrose is not hydrolyzed by an external invertase, the lack of a pH effect is not surprising but would also suggest little effect on pH on transport across the plasmalemma. However, the lack of a pH effect does not eliminate the possibility of proton co-transport of sucrose at the tonoplast (6, 12).

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