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Characterization of the Hexose Transport System in Maize Root Tips

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ABSTRACT

Sugar-depleted excised maize (*Zea mays* L.) root tips were used to study the kinetics and the specificity of hexose uptake. It was found that difficulties induced by bulk diffusion and penetration barriers did not exist with root tips. Several lines of evidence indicate the existence of a complex set of uptake systems for hexoses showing an overall biphasic dependence on external sugar concentrations. The results suggest that the high and the low affinity components might be located on the same carrier. One uptake system was specific for fructose, but the high affinity component was repressed by high concentrations of external glucose. A second system was specific for glucose and its analogs (2-deoxy-D-glucose and 3-*O*-methyl-D-glucose), and a third one, more complex, had a high affinity for glucose and its analogs but could transport fructose when glucose was not present in the external solution. A simple method is proposed to determine the inhibitor constants in competition experiments.

The seminal maize root tip has few carbohydrate reserves but is a strong sink for sugars. Therefore, its energy metabolism, either in normoxia through oxidative phosphorylation (18), or in anoxia through fermentation (19), is controlled by the level of sugar supply. The respiratory rate in sugar-depleted tips can be raised and stabilized at various values depending on the exogenous glucose concentration (18). Furthermore, subjecting maize roots to hypoxic conditions induces an increase in metabolism which implies a better utilization of the available sugars by anoxic cells (17).

These findings point out the importance of sugar transport for the cellular economy. Some characteristics of this transport were studied in maize root protoplasts. Glucose which appears to be the primary transported sugar, accumulates by multicomponent mechanisms (10), whereas sucrose is poorly transported as such and has to be hydrolysed by a cell wall invertase to allow the resulting hexoses to be taken up by the cells (7). However, many aspects of the hexose transport mechanisms in intact root tips remain unknown.

In this article, we provide a detailed investigation of the glucose and fructose transport systems and provide evidence for the presence of different carriers and mechanisms for the control of glucose and fructose uptake.

MATERIALS AND METHODS

Chemicals. All the unlabeled chemicals were purchased from Sigma Chemical Co. (St. Louis, MO) and were of the highest available purity. D-(U-^{14}C)glucose (11 GBq/mmol) was from Centre d'Etude Atomique, France; D-(U-^{14}C)fructose (11 GBq/mmol) was from Radiochemical Center, Amersham, England; 3-*O*-methyl-D-(U-^{14}C)glucose (11.7 GBq/mmol) and 2-deoxy-D-(1-^{14}C]glucose (2.15 GBq/mmol) were from New England Nuclear, Boston, MA.

Plant Material. Maize (*Zea mays* L. DEA) was germinated in the dark at 25°C on wet filter paper. At 3 d after imbibition, 3 mm primary root tips were excised and incubated for 4 h at 25°C in a mineral solution (18), aerated by air bubbling, and buffered by 5 mM MOPS[1] adjusted to pH 6.2 by KOH.

Transport Studies. Root apices were placed in groups of 20 in disposable syringes containing 1.8 mL of the above medium. Inhibitors (pCMBS, NEM, or FCCP)[1] were added as indicated. The syringes were fitted with 12 × 0.45 mm needles on vacuum rubber tubes flushed with air or N_2. After 15 min equilibration at 25°C, sugar uptake was initiated by addition of 200 μL of radioactive substrate to the desired final concentration. Unless otherwise stated, unlabeled and labeled sugars or competitors were added together. After appropriate times, the uptake was terminated by washing the tips five times for 1 min each with 20 ml of ice-cold MOPS solution. The ice-cold tips were counted by groups of 10 in 2 ml of aqueous scintillation fluid (ACS II, Amersham). All the determinations were done in duplicate.

Phosphorylation of 2-deoxy-glucose. Root tips were placed in groups of 40 in 2 ml of medium containing 1 mM [^{14}C]dGlc (65 MBq/mmol) as described above. After appropriate times they were rapidly rinsed three times within 20 s with ice-cold MOPS solution and immediately frozen in liquid N_2. The soluble sugars were then extracted with 0.6 M TCA as for adenine nucleotides (18). The extract was dried under vacuum and resuspended in 100 μL H_2O. One aliquot (10–20 μL) was used for the determination of the total radioactivity and a second (5–20 μL depending on radioactivity) was spotted and thin layer chromatographed as described previously (16). After a 7-d exposure period on a Kodak X-ray safety film ARD, two radioactive spots, corresponding to dGlc and dGlc-P, were located on the chromatogram and recovered for counting.

Determination of Fructose Carrier Inhibitor Constants. The experimental results obtained in the course of this work suggest that two different sets of fructose carriers were operating with similar affinities (K_m) for the substrate (Fig. 4, A and B). One set was not affected by the presence of competitors, whereas the other one could be completely inhibited. Dixon's representation of inhibition (6) which applies to a homogeneous population of enzyme, could not be used for the calculation of inhibitor constants of such a complex system. We have therefore, developed a simple mathematical and graphical method to describe this

[1] Abbreviations: pCMBS, *p*-chloromercuribenzene sulfonate; FCCP (*p*-trifluoromethoxy)carbonyl cyanide; NEM, *N*-ethylmaleimide; 3-OMG, 3-*O*-methyl-D-glucose; dGlc, 2-deoxy-D-glucose; MOPS, 3-(morpholino)propanesulfonic acid.

situation which can be quite common in uptake mechanisms (15).

If v is the velocity of the system in the absence of inhibitor and v_i the velocity in the presence of inhibitor, the fractional inhibition, I, can be defined by:

$$I = (v - v_i)/v \quad (1)$$

The velocity v is the sum of the velocity of the two sets of carriers:

$$v = v_1 + v_2 = V_m \cdot S/(K_m + S) \quad (2)$$

Where v_1 is the velocity of the carrier not affected by the inhibitors and v_2, the velocity of the carrier which can be inhibited. V_m and K_m are the kinetic constants of the system and S the concentration of the substrate (fructose).

In the presence of inhibitors only v_2 is affected, and there are two possibilities:

A. The inhibition is noncompetitive, then:

$$v_i = v_1 + (V_{m2} \cdot S/[K_m + S])(K_i/[K_i + i]) \quad (3)$$

where i is the inhibitor concentration and K_i its inhibition constant. Substituting Eqs. (2) and (3) in Eq. (1) we find:

$$I = (V_{m2}/V_m)(1 - K_i/[K_i + i]) = (V_{m2}/V_m)(i/[K_i + i]) \quad (4)$$

or

$$I = (V_{m2}/V_m) - (V_{m2}/V_m)(K_i/[K_i + i])(i/i) \quad (5)$$

Substituting Eq. (4) in Eq. (5) we find:

$$I = (V_{m2}/V_m) - K_i(I/i) \quad (6)$$

with $V_{m2}/V_m = I_{max}$. Finally we have

$$I = I_{max} - K_i(I/i) \quad (7)$$

which gives a simple linear relationship when I is plotted *versus* I/i. The slope is independent of the substrate concentrations and represents the absolute value of the inhibitor constant K_i.

B. The inhibition is competitive; now

$$v_i = v_1 + V_{m2} \cdot S/(K_m [1 + i/K_i] + S) \quad (8)$$

substituting Eqs. (8) and (2) in Eq. (1) it is possible to obtain the following equation:

$$I = V_{m2}/V_m - ([K_m + S]/K_m) K_i(I/i) \quad (9)$$

where $V_{m2}/V_m = I_{max}$.

Here, again, we have a linear relationship, but in this case, the slope varies with the substrate concentration. If the K_m is not previously known, it is necessary to do inhibition experiments using at least two different substrate concentrations in order to calculate the value of K_i.

It should be stressed that the Eqs. 7 and 9 were obtained assuming $K_{m2} \approx K_m$.

RESULTS AND DISCUSSION

Time Course of Sugar Uptake. Under our experimental conditions, the uptake of glucose, dGlc, fructose, and sucrose from a 10 mM external solution, remained linear for at least 60 min and extrapolated to the origin. This remained true even during very short time experiments with 1 mM dGlc (Fig. 1). However, the uptake of the nonmetabolizable analog of glucose, 3-OMG only remained linear for 10 min under the same conditions. This phenomena was not observed in isolated maize protoplasts (10). It may be that flux equilibrium was approached more rapidly in protoplasts than in root tips. These results indicate that the solutes in the free space were readily eliminated by the rinsing procedure. The absence of a lag in the uptake rate was surprising and suggests either that exogenous sugars could very rapidly penetrate the free space in the thickness of the tissues, or, that they did not enter the tissues via the apoplast; the uptake being only into the external cell layer.

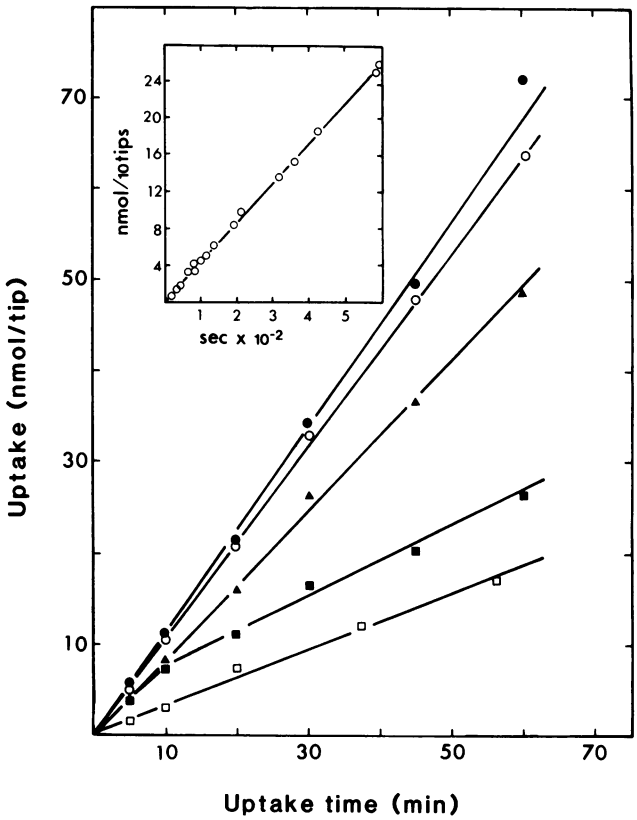

FIG. 1. Time course of carbohydrate uptake by 5 mm excised maize root tips previously sugar depleted by 4 h of aging. The external concentration of glucose (●), dGlc (○), fructose (▲), 3-OMG (■) and sucrose (□) was 10 mM. Inset: Time course of 1 mM dGlc uptake in a short time experiment. The fresh and dry weight of one tip were 2.15 and 0.29 mg, respectively.

Among the sugars assayed, the highest uptake rate was always observed with glucose whereas sucrose was poorly transported. Other experiments (data not shown) confirmed results previously found with corn root protoplasts (7, 10) showing that sucrose is poorly transported as such, but has to be hydrolyzed first by the cell wall invertase which appears to be the rate limiting step of its transport. For that reason this study focused only on hexose transport.

Kinetics of Sugar Uptake. Typical responses to increasing external concentrations of glucose and fructose are shown on Figure 2. The two sugars had complex kinetics, similar to those reported in corn root protoplasts (10) and many other plant materials (10). In the Eadie-Hofstee representation over a wide range of concentrations (Fig. 2), it was evident that multicomponent systems (15) were operating in the uptake of all the sugars studied; however, the overall pattern of transport appears to be biphasic, corresponding to low and a high affinity system.

According to the Eadie-Hofstee equation, $v = V_{max} - K_m (v/S)$, the transport parameters of the uptake systems were calculated for the different sugars or analogs studied (Table I). The K_m for glucose, 3-OMG and dGlc were very similar and close to 0.7 and 50 mM for the high and low affinity components, respectively. It is worth noting that dGlc which was immediately phosphorylated as shown in Figure 3, had a V_{max} similar to glucose which is known also to be very rapidly phosphorylated, whereas the V_{max} of the nonmetabolizable analog 3-OMG was lower probably because net flux inward was diminished by efflux

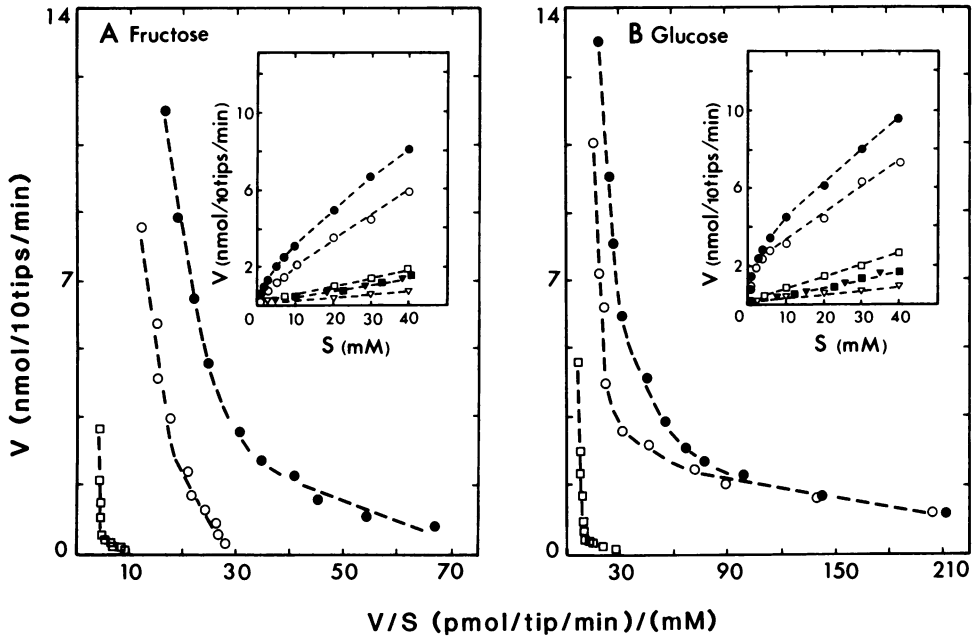

FIG. 2. Eadie-Hofstee plot and classical representation (inset) of fructose (A) and glucose (B) kinetics of uptake in the presence of various inhibitors. The labeled sugars were added 5 min after the inhibitors or after 30 min bubbling of the incubation medium with gaseous N_2 in the anaerobic treatments. Symbols: control without inhibitors (●); 2 mM pCMBS (○); 1.5 mM NEM (□); anaerobiosis (▼); 20 μM FCCP (■); anaerobiosis plus 2 mM pCMBS (▽). The fresh and dry weights of one tip were 2.15 and 0.29 mg, respectively.

Table I. *Kinetic Parameters for the Uptake of Glucose, 3-OMG, dGlc, and Fructose by Excised Maize Root Tips*

The uptake lasted 10 to 15 min. The K_m (mM) and the V_{max} (pmol tip^{-1} min^{-1}) values were obtained from the quasilinear portion of the Eadie-Hofstee representation. The concentration ranges used for the determination of the parameters of the high-affinity components were 0.5 to 3 mM for glucose, 3-OMG and dGlc, and 1 to 7 mM for fructose. For the low affinity component they were 20 to 70 mM. The fresh and dry weight of one tip were 2.15 and 0.29 mg, respectively.

Sugars	High-Affinity		Low-Affinity	
	K_m	V_{max}	K_m	V_{max}
Glucose	0.8 ± 0.2	301 ± 24	45 ± 15	1984 ± 515
3-OMG	0.7 ± 0.1	172 ± 10	53 ± 7	1016 ± 112
dGlc	0.7 ± 0.1	300 ± 5	48 ± 11	1721 ± 250
Fructose	5.9 ± 0.7	362 ± 58	98 ± 11	2527 ± 513

to a greater extent than with other sugars. This finding suggests that sugar transport in maize root tips may be loosely coupled to phosphorylation, as proposed in sugarcane (4), and in mammalian cells, yeast and bacteria (13).

The kinetic parameters of fructose transport differed markedly from those of glucose with higher K_m values of 6 and 100 mM for the high and the low affinity components, respectively, suggesting that fructose may be transported by a different system.

Effects of Sulfhydryl Reagents. The effects of the membrane impermeant pCMBS (2 mM) and those of the membrane permeant NEM (1.5 mM) on the uptake of fructose and glucose are illustrated in Figure 2, A and B, respectively. The pCMBS did not inhibit glucose uptake at concentrations of glucose up to 3 mM and was a poor inhibitor for higher concentrations (only 30% at 20 mM external glucose; inset, Fig. 2B). The values of the slopes of the linear portions of the Eadie-Hofstee representation, show that the K_ms of both the low and the high affinity components were not modified, indicating that pCMBS reacted with sulfhydryl groups other than those involved in glucose binding and transport.

The effect of sulfhydryl reagents on fructose uptake was more pronounced at low concentrations of fructose and the K_m of the high affinity component increased from 5 to 20 mM in presence of pCMBS (Fig. 2A). This suggests that the binding site of fructose is different from that of glucose and has sulfhydryl groups which

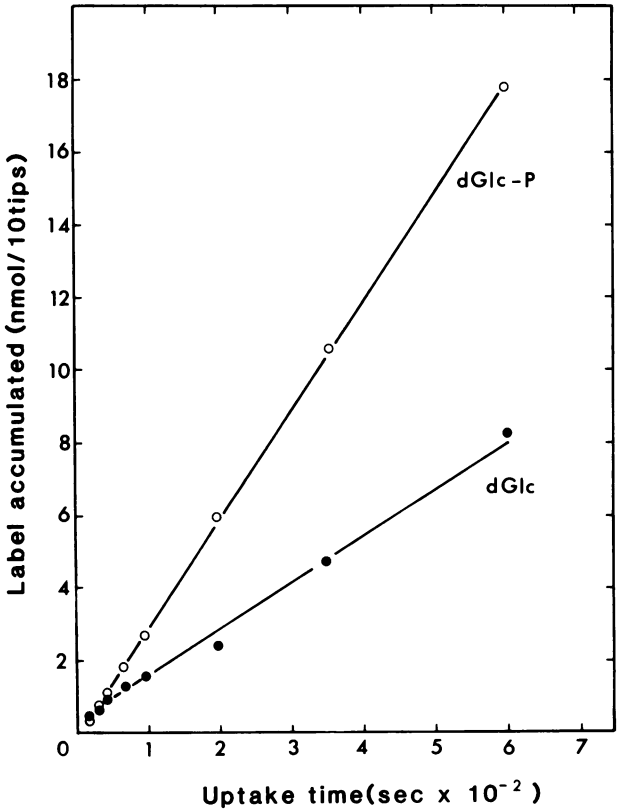

FIG. 3. Time course of the appearance of dGlc-P within the tissues during short uptake experiments in presence of 1 mM dGlc. After a 20 s rinsing, the soluble sugars were extracted and separated by TLC as described in "Materials and Methods." The fresh and dry weights of one tip were 2.15 and 0.29 mg, respectively.

react with pCMBS. However, the overall inhibition of fructose transport by pCMBS remained low and similar to that of glucose at higher substrate concentrations (30% inhibition at 20 mM external fructose).

Inhibition by the membrane permeant NEM was strong for both glucose and fructose uptake and similar to that obtained

with the uncoupler FCCP and with N_2 (insets, Fig. 2, A and B). The uptake rate was dramatically decreased by NEM but the low and high affinity components were still present. This indicates that the transport was affected by the inhibition of energy metabolism more than a direct effect on the carriers. The evidence for a carrier-mediated transport operating even at a low level of cellular energy metabolism was reinforced by the additional inhibition obtained with 2 mM pCMBS in absence of oxygen (inset, Fig. 2, A and B).

Substrate Specificity. In order to determine the specificity of the transport systems, reciprocal competition experiments were carried out between the different sugars and analogs. The results of this study are reported in Table II. It is clear that D-glucose, dGlc, and 3-OMG were each strong competiting inhibitors of each other and that they also inhibited the transport of fructose. This supports a common transport system from glucose and its analogs and an interaction of these sugars with the transport of fructose. However, the most significant result was the absence of competition of fructose with all these sugars even at high relative concentrations. A quantitative check has been done: taking the K_m values given in Table I according to the concentrations reported in Table II and inserting them in the classical equations formulating inhibition, 16 to 73% inhibition would be predicted. These values are considerably above the experimental error. In our experiments, such values were never observed (Table II). This result implies that fructose did not share a common binding site with glucose or induced any indirect inhibition of this transport. Therefore, the inhibition of fructose transport by glucose and its analogs cannot be attributed to a competition for its binding site but presumably to some indirect modification of the fructose carrier. These conclusions remained true in the absence of oxygen.

Uptake of Fructose. In order to obtain more information on the fructose transport system, we studied the kinetics of fructose uptake in the presence of excess of glucose, dGlc, and 3-OMG (Fig. 4, A and B). The K_m values of both high and low affinity components were not modified in the presence of 40 mM 3-OMG, but the V_{max} values were about half the control. Even at 100 mM 3-OMG or dGlc, the high affinity component was not affected (Fig. 4B). With glucose, the K_m values of neither the low nor the high affinity component were modified for concentrations lower than 40 mM (data not shown) but for higher concentrations of glucose the high affinity component was completely abolished (Fig. 4B). Similar observations were made for the glucose transport system in yeast and in fungi (3, 12). It should be noted that in root tips maintained in 100 mM glucose after excision and rinsed before transport measurement, the low K_m component of fructose uptake was not affected (Fig. 4B). This observation suggests that the metabolites produced subsequent to glucose metabolism are not involved in the repression of fructose uptake. These results indicate that 3-OMG, dGlc, and glucose at low concentrations did not compete with fructose for its binding site, the affinity of the two components being unmodified, but they did reduce the total number of carriers available for fructose transport, decreasing the apparent V_{max}. This reinforces the idea that two different systems are operating for fructose transport as shown later.

The disappearance of the low K_m transport system of fructose at high external glucose concentrations can be correlated with the ability of glucose to be phosphorylated after uptake. It is therefore tempting again to make a parallel with the uptake system of yeast (1, 2, 9) in which it has been established that the low K_m component of hexose uptake depends on the presence of the hexokinases. It may be that glucose, after entering the cell, diverts the activity of the hexokinases which have a higher affinity for glucose than for fructose (8, 20). That would agree with the observation that the disappearance of the low K_m component of fructose transport occurred only at high external concentrations of glucose (>40 mM). The fact that dGlc did not induce a similar inhibition may be attributed to its lower affinity for hexokinase. However, having no mutants for the hexokinases, as in yeast, it is not possible at present to give a direct demonstration of this mechanism for plant tissues. A better understanding of this mechanism will require more detailed investigations.

Inhibitor Constants of the Fructose Transport System. The uptake of fructose at concentrations ranging from 5 to 75 mM was measured in the presence of eight concentrations of glucose, 3-OMG, and dGlc ranging from 0 to 20 mM, in order to calculate the inhibition constant (K_i) and the maximum inhibition (I_{max}) as described in "Materials and Methods." The data reported in Table III show that, in the range of experimental errors, the values found for the slope of the linear relationship obtained when I is plotted versus I/i were independent of substrate (fructose) concentrations. Therefore, the inhibition of fructose uptake by glucose and its analogs is noncompetitive which provides an additional evidence that glucose and fructose did not share a common binding site and the absolute value of the slope represents the inhibitor constant K_i. As demonstrated previously, K_i is an accurate measurement of the affinity of inhibitors in sugar transport studies (5). The values found with glucose, 3-OMG, and dGlc were each close to the K_m values of their high affinity transport system. This result indicates that fructose and glucose shared a common carrier with different binding sites for both sugars and that the binding site of glucose was also an inhibitory site for fructose. Consequently, this system could transport fructose only in the absence of glucose. It should be noted again that the maximum inhibition obtained for fructose transport was close to 50% whatever the fructose concentration. This result indicates that the same carriers were operating over the full range of external concentrations for fructose transport, supporting the idea that a single carrier might present different affinities according to the substrate concentration (12, 14). The remaining 50% always remained uninhibited. These results imply the operation of an additional carrier highly specific for fructose and not directly affected by the presence of glucose or its analogs even at relatively high concentrations.

Table II. *Reciprocal Competition between Different Sugars under Aerobic and Anaerobic Conditions*

Root tips were incubated in the buffered medium bubbled with air or N_2 for 30 min. The labeled sugars were added just after the competitors and the uptake lasted 15 min. The inhibition was calculated as described in "Materials and Methods."

Labeled Sugars	Competitors	Inhibition of Uptake	
		Air	N_2
mM			
Fructose (10)	Glucose (2)	0.34	0.35
	dGlc (2)	0.33	0.34
	3-OMG (2)	0.33	0.18
dGlc (10)	Glucose (20)	0.48	0.40
	3-OMG (20)	0.50	0.26
	Fructose (20)	0	0
3-OMG (10)	dGlc (20)	0.32	NT[a]
	Fructose (20)	0.001	NT
Glucose (30)	Fructose (30)	0.02	NT
Glucose (2)	Fructose (10)	0.06	0.08
	dGlc (4)	0.28	0.23
	3-OMG (4)	0.51	0.19
Glucose (0.5)	Fructose (25)	0.005	NT

[a] Not tested.

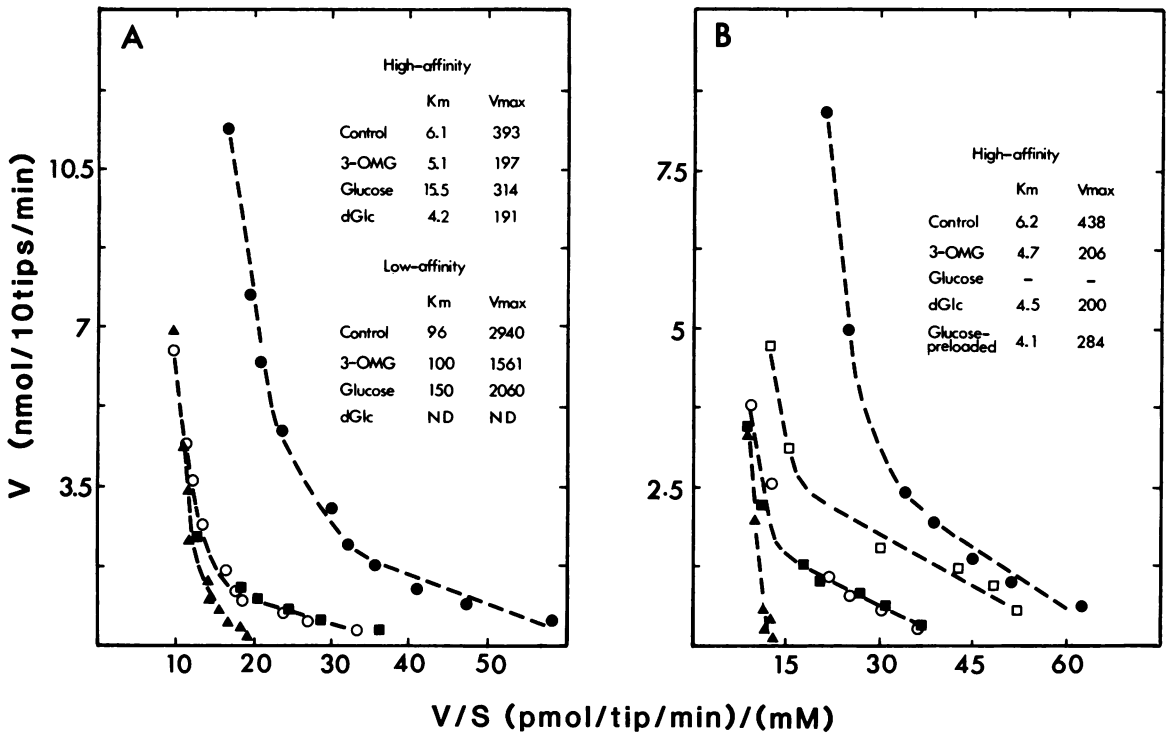

FIG. 4. Eadie-Hofstee plots of fructose uptake by 3 mm excised maize root tips. A, Sugar-depleted root tips (the labeled fructose ranged from 1–70 mM): control in absence of other external sugars (●); in presence of 40 mM glucose (▲) or 3-OMG (○), or dGlc (■). B, Labeled fructose ranging from 1 to 40 mM: root tips preloaded 4 h in 100 mM glucose and incubated after rinsing in the absence of other external sugars (□); sugar-depleted root tips: control in the absence of other external sugars (●); in the presence of 100 mM glucose (▲) or 3-OMG (○) or dGlc (■). The fresh and dry weights of one tip were 2.15 and 0.29 mg, respectively. ND, not done.

Table III. *Inhibition Parameters of Glucose, 3-OMG, and dGlc on the Uptake of Fructose at Various Concentrations*

Concentrations of competitors ranging from 0 to 20 mM (i) were used to determine the fractional inhibition (I) of fructose uptake at the desired concentrations as described in "Materials and Methods." Competitors were added into the incubation medium just before the labeled fructose. Uptake lasted 10 or 15 min. The values presented in this Table were obtained graphically by plotting I *versus* I/i as described in "Materials and Methods." The values of the slopes (mM), in the range of experimental error, were independent of fructose concentrations and therefore their absolute values represent the inhibitor constant, K_i.

Labeled Fructose	Inhibition Parameters					
	Glucose		3-OMG		dGlc	
mM	[slope] = K_i	I_{max}	[slope] = K_i	I_{max}	[slope] = K_i	I_{max}
5	0.84	0.54	0.44	0.45	0.56	0.43
10	0.78	0.50	NT[a]	NT	0.79	0.50
20	0.81	0.53	0.37	0.47	0.69	0.48
75	0.52	0.46	0.49	0.47	0.48	0.43

[a] Not tested.

CONCLUSIONS

One of the main objections raised against the use of intact tissues instead of cell or protoplast suspensions for kinetic studies, lies in the presence of bulk diffusion problems and penetration barriers (11). The absence of a lag in the uptake and the similarity of the values found for the K_i of glucose on fructose uptake and the K_m of glucose transport show that such difficulties did not exist with maize root apices which behaved like a simple giant cell. We have no data to decide whether the sugars actually penetrate the free space inside the tissues or not, but the results obtained demonstrate that excised maize root tips were well adapted to the purpose of the present work. We do not mean that protoplasts do not offer a number of distinct advantages as emphasized (11), but as far as kinetic and specificity studies are concerned, intact root tips were easier to use and eliminated possible artefacts due to the fragility of a biological material obtained after long and tedious preparation.

The results presented here indicate the existence of a complex

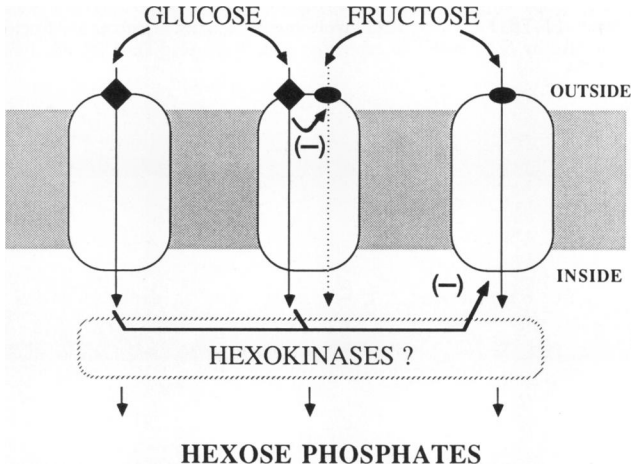

FIG. 5. Tentative model for the transport of hexoses and their interactions in maize root tips. Three kinds of carriers are proposed. (A) and (B), Specific for glucose and fructose, respectively; (C), common for both hexoses with distinct binding sites for fructose and glucose but the binding of glucose induces some modifications of the carrier which prevent the transport of fructose. Fructose can therefore be transported by this carrier only in absence of glucose. The model indicates also the repressive effect of glucose on the high affinity component of the specific fructose carrier in connection with hexokinase activity.

set of uptake systems for hexoses. One was specific for fructose, another for glucose, and a third one had a high affinity for glucose but could transport fructose when glucose was not present in the external solution. The main conclusions are summarized in Figure 5. They are based on the following considerations. First, glucose and its analogs (3-OMG, dGlc) had similar kinetic parameters and were strong competitors for each other which implies a common carrier. Second, the kinetic parameters for fructose were very different and it was not a competitor for glucose or its analogs. Third, the inhibitory effect of the impermeant sulfhydryl pCMBS was different for glucose and for fructose. Fourth, 3-OMG, dGlc, and glucose at low concentrations blocked, noncompetitively, up to 50% of the fructose transport but no more. Fifth, the binding site for glucose and its analogs when acting as inhibitors of the uptake of fructose had the same characteristics as the high affinity binding site of glucose on its own carrier. This site was therefore different from the binding site of fructose. Sixth, when glucose was added separately in the external medium, the V_{max} of glucose uptake was approaching that of fructose. This implies the operation of an additional transport system specific for glucose.

The strong competing effect of glucose over other sugars and the relative inability of these sugars to compete with glucose, have been reported a number of times for a variety of tissues (for review, see Ref. 15). However, little quantitative work has been done on this subject and the overall picture of sugar transport remains unclear partly because the classical methods for the determination of inhibitor constants in competition experiments do not apply to complex enzymic systems. The model proposed in the work for glucose and fructose uptake clarifies the pattern of hexose competition, in maize root tips at least, and may apply to a number of other substrates and tissues.

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