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Re-sorption of organic compounds by roots of *Zea mays* L. and its consequences in the rhizosphere

III. Characteristics of sugar influx and efflux

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Abstract

The influx and efflux of sugar-C and the cycling of C within intact maize roots (*Zea mays* L.) was studied in sterile solution culture. Using metabolic inhibitors it was shown that roots could take up sugars against the concentration gradient probably via H^+-ATPase dependent plasmalemma proton cotransporters. In contrast to this, no evidence was found for an ATPase mediated efflux of sugars from the root. All parts of the root were capable of taking up exogenous sugars. Examination of sugar exudation sites along the root slowed efflux at all locations, with the amount of efflux linearly correlated with internal cellular concentration. The results clearly indicated that the influx-efflux mechanisms are linked both spatially, temporally and with respect to the sugars capable of transportation. The turnover of C within the root was found to be extremely rapid with turnover of the soluble sugar pool being 0.8 to 15 times daily depending on root spatial location. The results strongly suggest that the recapture of sugars from outside the root plays an important role in regulating the amount of C lost to the soil which in turn will reduce both pathogen attraction and the size of the rhizosphere microbial population and will also increase the plant's C efficiency.

Introduction

It is now widely accepted that the exudation of C compounds from the roots into the soil accounts for a considerable part of C flow within the plant. On average, 13% of the plant's net fixed C is lost in this way (Klein et al., 1990; Whipps, 1990). Although numerous authors have attempted to quantify the amount of rhizodeposition and the constitutive compounds within the rhizosphere, little is still known about the exudation process itself. It is currently thought that the release of low molecular weight soluble compounds results from passive leakage through the plasma membrane and from damage of root hairs and epidermal cells (Whipps, 1990).

In previous rhizodeposition investigations it has always been assumed that once C compounds are lost from the root they are irretrievable (e.g. Kraffczyk et al., 1984; for a review see Curl and Trueglove, 1986): however, it has recently been ascertained that this is an oversimplification of root-soil C fluxes. In studies made by Jones and Darrah (1992, 1994) and Von Wiren et al. (1994) it has been demonstrated that the influx of soluble low molecular weight C may play an important role in regulating the amount of C lost by the root. The active uptake of sugars and amino acids by green plants was first demonstrated by Komor (1973) with uptake via both specific and non-specific plasma membrane bound carriers requiring a proton motive gradient produced by the plasma membrane H^+-ATPase (Bush, 1993; Briskin and Hanson, 1992). Most of the work performed to date has focused on excised above

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ground tissues employing higher sugar concentrations than those found within the soil and usually with reference to phloem loading/unloading and is therefore of limited relevance to a root-soil interface situation.

The influx of C compounds has important implications for many of the applied research aspects of the rhizosphere including the re-sorption of organo-metallic chelates, plant signalling and regulation of the microbial populations within the rhizosphere. As sugars form the principle component of soluble root exudates the aim of this study was to determine the characteristics of sugar-C influx and efflux from maize roots. The flow of C within the root itself will also be considered.

Materials and methods

Plant culture

Seedlings of *Zea mays* L. (c.v. LG 11) were prepared and grown under sterile conditions as described in Jones and Darrah (1992). The plants were grown in sterile, hydroponic culture in a climate chamber with a day/night rhythm of 25/18 °C, 16 hour photoperiod and light intensity of 800 μE $m^{-2}s^{-1}$. All experiments were performed under sterile conditions in at least triplicate. Sterility checks at the end of experiments were made by plating out 110 μL aliquots of root-bathing solution onto nutrient agar and incubating the plates at 25 °C for seven days.

Effect of metabolic inhibitors on sugar influx and efflux

Metabolic inhibitors were used to determine whether the transport of the non-metabolizable glucose analogue, 3-O-methyl-D-glucopyranose (3-OMG), across the plasmalemma was transporter linked or occurred purely by passive leakage. The inhibitors (Sigma Chemical Co.) and their concentrations were as follows: A. Control (no inhibitors), B. carbonyl cyanide m-chlorophenyl-hydrazone (CCCP; 10 μM), C. p-chloromercuri-phenylsulfonic acid (pCMBS; 100 μM), D. N-ethylmaleimide (NEM; 500 μM), E. Temperature (5 °C).

(a) Influx

In the influx studies, intact roots of 7 day-old plants were placed in individual Petri-dishes containing 25 mL of 10% Hoaglands solution containing one of the inhibitors. In treatment E (5 °C), solutions and plants were cooled for 150 minutes prior to the start of the experiment. After 30 minutes of incubation with the inhibitors, 850 Bq of [^{3}H]3-OMG (Du Pont, 2.22–3.33 TBq $mmol^{-1}$) was added to the root-bathing medium to give a final concentration of 100 μM and the plants left in a sterile laminar flow cabinet for 3 hours. In the low temperature treatment (E) plants were placed in a refrigerator at 5 ° C for 3 hours. After the uptake period, the plants were washed twice for 5 minutes in 40 mL of unlabelled 10% Hoaglands solution. The amount of [^{3}H] label taken up by the roots was then measured by serially extracting them with 5 mL of 100% ethanol and 20% ethanol for 30 min at 80 °C. Radioactivity was counted by liquid scintillation in a final volume of 20 mL with Beckman Ready-Gel scintillation fluid.

The fate of newly re-sorbed label was assessed by following the movement of 3-OMG into and out of root cells with time. Five excised 10 mm root tips were incubated in 1 mL of a 10% Hoaglands solution containing 1.6 kBq of [^{3}H]3-OMG (100 μM) for periods of 15, 30, 60, 90, 120 or 180 minutes. After incubation, the root tips were removed from their loading solution and washed twice for 3 minutes in 10% Hoaglands solution. Efflux of label from the tips was then measured by placing them in 1 mL of a 10% Hoaglands solution containing no 3-OMG, and withdrawing the wash solution at 15 minute intervals over 45 minutes. After 45 mins the amount of label remaining in the roots was assayed as described above.

(b) Efflux

In the efflux studies, intact roots were loaded in a 10% Hoaglands solution (35 mL) containing 37 kBq of [^{3}H]3-OMG (100 μM) for 6 hours. After loading, the roots were washed twice for 5 minutes in an unlabelled solution to remove apoplastic and surface associated label (DiTomaso et al., 1992; Farrar, 1985). The plants were then transferred into individual Petri-dishes (25 mL solution) containing no 3-OMG but one of the above inhibitors (A to E). In the following 2 hours, plants were transferred every 15 minutes to a new solution containing inhibitor and the amount of 3-OMG exuded was measured by liquid scintillation. After 2 hours the amount of residual 3-OMG remaining in the roots was extracted as described above.

Spatial characteristics of efflux

Eight day-old plants were transferred to Petri-dishes containing 25 mL of 10% Hoaglands solution and 20 kBq of [^{3}H]3-OMG (2.22 m*M*). The root systems were then left to take up 3-OMG over a period of 22 hours (25 °C, 100% RH, 40 μE m^{-2}s^{-1}). The roots were then washed twice in 30 mL of unlabelled nutrient solution for periods of five minutes to remove any apoplastic and surface located 3-OMG. Plants were then transferred to 14 cm diameter Petri dishes, in which 2 cm long sections of 5 mm diameter plastic tubing were threaded along the root length and filled with $\approx$ 0.2 mL of nutrient solution which was held in the cylinders by capillarity. Five-mm gaps were left between root segments to prevent the mixing of samples. Tests where dyes were introduced into the tubes indicated that errors due to solution mixing were small (< 10%). At 15 minutes and then at 30 minute intervals, the solution contained within the sections was pipeted out and replaced. After a 210 minute efflux period, the amount of label remaining in the root sections was measured as described above. Efflux solutions and root extracts were counted by liquid scintillation.

Selectivity characteristics of influx

Intact roots of 14 day old plants were placed in a 10% Hoaglands solution (30 mL) containing all of the following sugars at a concentration of 100 μ*M* (glucose, mannose, ribose, rhamnose, fructose, xylose, arabinose and galactose). At times of 3, 5, 7, 12, and 24 hours, 1.5 mL aliquots were removed from the root-bathing medium and immediately frozen. Samples were freeze dried overnight and TMS-oxime derivatives of the sugars prepared according to Sturgeon (1990; Method Bc). Derivatized samples were then analyzed on a Pye-Unicam 108 capillary column gas chromatograph (GC) with temperature program of 150 °C (5 min) and 150 to 310 °C (2 °C min^{-1}) using adonitol as an internal standard. Sugar concentrations were calculated from peak areas.

Concentration of compounds inside the root

Main root axes of 10 day-old plants were sectioned into 1 cm pieces and serially extracted with 100% and 20% ethanol (20 minutes, 80 °C) and the extracts bulked. The spatial distribution of sugars was then measured by gas chromatography as described above.

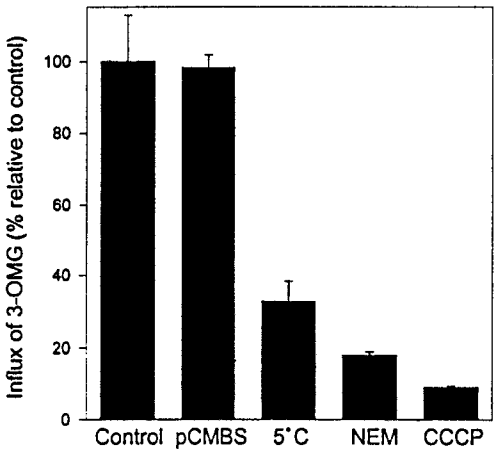

Fig. 1. The effect of various metabolic inhibitors on the influx of [^{3}H]3-OMG into intact maize roots from a 100 μ*M* solution over a 3 h period. Data are means ± s.e.

Measurement of root respiration

Root respiration, as an estimate of metabolic activity, was measured along the length of 8 day-old maize roots using a temperature controlled (25 °C) Hansatech oxygen electrode. Starting at the root tip, five sterile 5 mm root sections were excised and inserted into the 10% Hoaglands solution filled cavity of the oxygen electrode. The influence of wounding (assayed by cutting 2 cm root sections into 2, 4 or 8 pieces and measuring respiration) and microorganism contamination (background respiration after removal of roots) on the measurement of root respiration was found to be minimal.

Results

The effect of metabolic inhibitors on sugar influx and efflux

The inhibitors used in this study (CCCP, NEM and pCMBS) have all been shown at the concentrations employed not to affect membrane integrity (DiTomaso et al., 1992; Fieuw and Patrick, 1993; Komor et al., 1978, 1982; Porter et al., 1985). They were used to assess the factors controlling sugar transport in intact maize roots.

(a) Influx

The presence of the oxidative respiration uncoupler and protonophore, CCCP, resulted in low levels of 3-

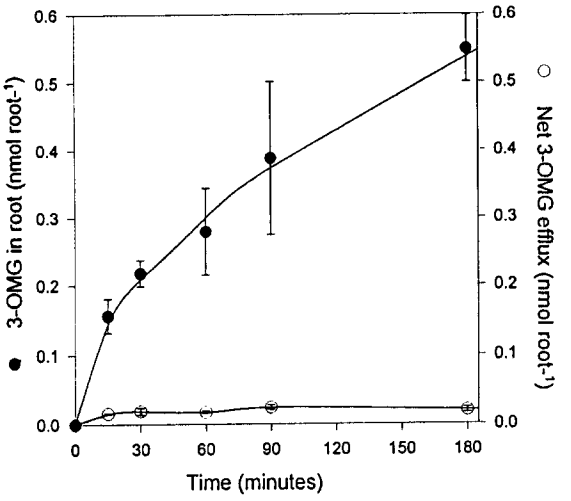

Fig. 2. The effect of loading time on the accumulation of [^{3}H]3-OMG within excised maize root tips (closed symbols) and the subsequent amount of efflux at each lime point after transfer of the tips to an unlabelled solution for 45 mins (open symbols). Data are means ± s.e.

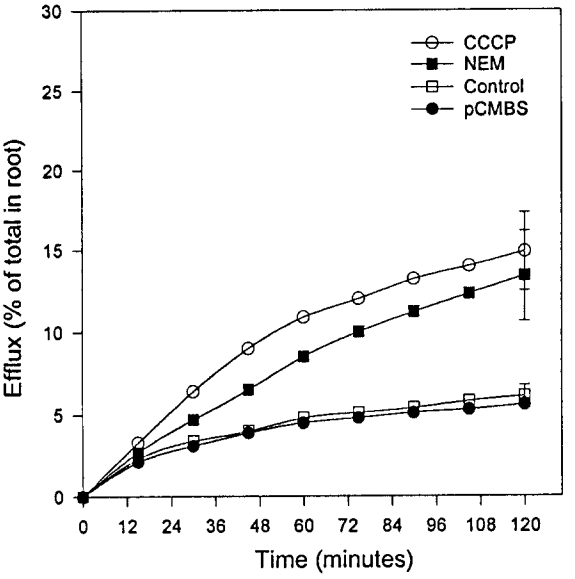

Fig. 3. The effect of various metabolic inhibitors on the efflux of [^{3}H]3-OMG from intact maize roots over a 2 h period. Data are means ± s.e.

OMG accumulation within the roots suggesting that the plasmalemma electrochemical H^+ gradient, generated by the H^+-ATPase, is necessary for the movement of sugar into the root (Fig. 1). The membrane-permeable, covalently binding, non-specific sulfhydryl reagent, NEM resulted in a 82% inhibition of 3-OMG accumulation within roots compared with control plants. The small amounts of label accumulated in the presence of CCCP and NEM can be attributed to passive diffusion from the external solution into the root. The addition of the charged, non-plasmalemma-permeable membrane transport inhibitor pCMBS, resulted in no apparent inhibition of 3-OMG accumulation, suggesting that apoplastic enzymes and exposed plasmalemma protein -SH groups are not involved in the passage of hexoses across the plasma membrane. Incubation of the roots at low temperature (5 °C) inhibited glucose uptake by 67%. As the rate of influx was sensitive to a collapse of the plasmalemma H^+ gradient and to the inactivation of membrane proteins it suggests that influx occurs via an energy dependent plasmalemma transporter.

The effect of loading time on the pattern of 3-OMG influx and efflux from excised root tips is shown in Figure 2. As expected the level of 3-OMG in the root tips increased with time over the 3 h incubation period. Despite this constant increase in the root's 3-OMG content however, no corresponding increase in the amount of 3-OMG efflux was observed at any of the sampling times over the 3 h period on transfer to an unlabelled incubation medium. As root exudation of 3-OMG occurred at a near constant rate, it suggests that cytoplasmic 3-OMG levels were also remaining constant and that levels of 3-OMG in the cytoplasm were being actively regulated.

(b) Efflux

The effect of metabolic inhibitors on the rate of 3-OMG efflux from maize roots is shown in Figure 3. The amount of sugar taken up by the roots before inhibitor addition was similar for all plants, however, the rate of efflux was highly dependent on inhibitor treatment. The presence of CCCP and NEM increased the rate of 3-OMG efflux about two fold compared to control plants, with a 15 and 13% loss of label respectively over the 2 h efflux period. The higher rates of efflux observed in the presence of NEM and CCCP in comparison to the control treatment is probably a result of both tonoplast and plasmalemma transporters involved in the inward movement of glucose being inhibited. This would cause: (i), the prevention of the cell shuttling 3-OMG from the cytosol back into the vacuole thereby increasing cytoplasmic concentrations and (ii), the prevention of influx at the plasmalemma, preventing recapture of effluxed 3-OMG. This is in contrast to control plants where considerable accumulation within the vacuole can be expected, reducing

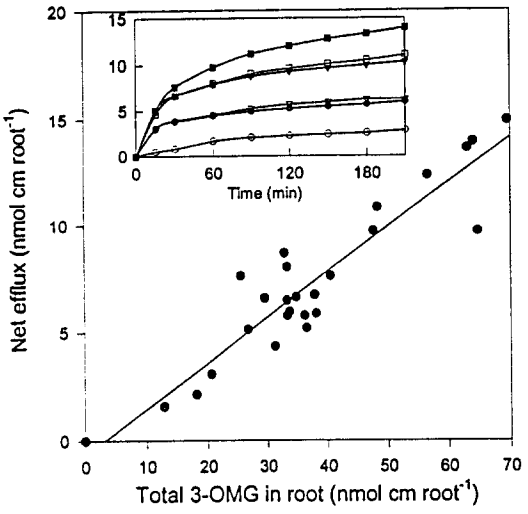

Fig. 4. The relationship between the level of 3-OMG accumulated in intact root sections during a 22 hour influx period and the subsequent efflux when transferred to an unlabelled root-bathing solution for 210 minutes. Inset are the 3-OMG efflux curves for the individual root sections. In, distance from root tip, the efflux sections were: ○, 0 to 20 mm; ●, 25 to 45 mm; ▽, 50 to 70 mm; ▼, 75 to 95 mm; □, 100 to 120 mm; ■, 125 to 145 mm. Scales on the y axes are the same for both graphs.

cytoplasmic efflux over time. As with influx, the presence of pCMBS had little effect on 3-OMG leakage. As efflux was not reduced in the presence of any of the metabolic inhibitors tested, it suggests that efflux was not energy coupled.

Spatial characteristics of efflux

After 22 h, the root accumulated high levels of 3-OMG (7 to 28 m*M*) at all locations resulting in a final root-solution m*M* concentration difference of between 5.2 and 17.0. The spatial distribution of sugar efflux along the root length was measured by following the efflux of [^{3}H]3-OMG from different root sections. The amount of 3-OMG lost over the subsequent 210 minute efflux period was very closely correlated with the total amount of label within the tissue (Fig. 4) indicating that the membrane permeability of the root to sugars was similar for all areas of the root. The data also showed that all areas of the root were capable of sugar uptake.

Selectivity characteristics of influx

During the 24 h uptake period all the sugars were taken up simultaneously, however, the rate of uptake was

Table 1. Uptake rate of individual sugars by intact maize roots. Maize roots were placed in an external solution containing all the listed sugars at a concentration of 100 μM for 24 h. Values are expressed as means ± s.e.. Data calculated from t = 24 h time points

Sugar	Uptake rate (nmol mg^{-1} root d^{-1})	% of glucose rate
Glucose	59 ± 1	100%
Mannose	49 ± 2	83%
Xylose	47 ± 1	80%
Arabinose	45 ± 2	76%
Galactose	36 ± 3	61%
Fructose	30 ± 1	51%
Ribose	15 ± 2	25%
Rhamnose	14 ± 1	24%

solute specific (Table 1) producing the following net uptake series: glucose > mannose = xylose = arabinose > galactose > fructose > ribose = rhamnose. After 24 hours, most of the glucose had been taken up by the root with the resultant concentrations in solution being 10 μM respectively, close to the influx-efflux equilibrium concentration calculated from Kraffczyk et al. (1984). The results indicate that the influx process is capable of taking up a wide range of sugars from outside the root. The results clearly demonstrated that sugars could be taken up by roots against the concentration gradient (e.g. root glucose concentration ≃ 72 m*M*).

Concentration of compounds along the root

The amount of sugars along the main root axes showed a distinct spatial pattern with the highest sugar levels observed just behind the root tip (Fig. 5). The mean root sugar concentrations (nmol sugar cm^{-1} root) were: glucose (321), fructose (42), sucrose (35), ribose (0.8), arabinose (0.4) and xylose (0.2). Levels of mannose, galactose, maltose, fucose and rhamnose were all below 0.1 nmol sugar cm^{-1} root. If the cell is assumed to possess an equal concentration of the above mentioned sugars in both the cytoplasm and the vacuole, the mean concentration of total sugars inside the root can be estimated at 86 m*M*.

Comparison of the root sugar concentrations with those found outside the root at the influx-efflux equilibrium point (see Jones and Darrah, 1993; i.e. rate

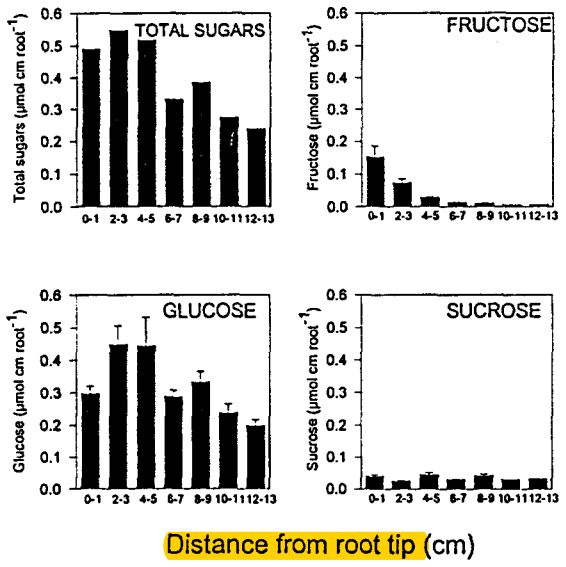

Fig. 5. The concentration of total sugars, glucose, fructose and sucrose along the main root axes of maize. Data are means ± s.e.

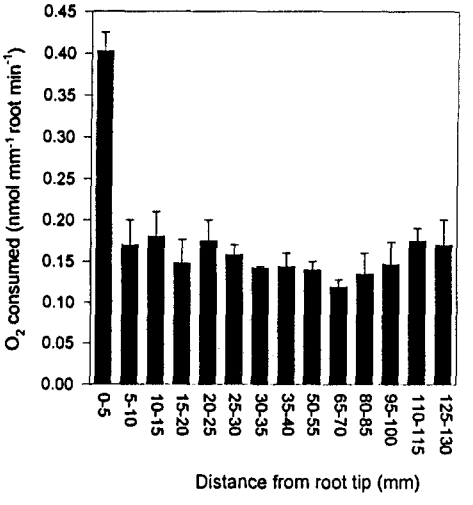

Fig. 6. The rate of respiration along the length of maize roots. Data are means ± s.e.

of influx = rate of efflux = no net release) indicate an accumulation ratio of 369 for glucose, 304 for fructose and 1267 for sucrose, providing strong evidence for the high efficiency of the sugar recapture mechanism.

Root C budget

Oxygen consumption over time was used to provide an accurate assessment of sugar and carbon turnover within the root cells. As expected, the highest rates of respiration were recorded at the root tip where the demand for photosynthate is highest (0.40 ± 0.02 nmol O_2 mm^{-1} root min^{-1}) (Fig. 6). Behind the root tip the rate of oxygen consumption was significantly lower but remained almost constant along the root length with an uptake: rate of 0.15 ± 0.01 nmol O_2 mm^{-1} root min^{-1}. As minimal cell division occurs behind the root tip, oxygen uptake within this region can be attributed to maintenance and ion uptake.

If it is assumed that during the aerobic respiration of glucose, with CO_2 and H_2O as the sole end products, the ratio of oxygen consumption:glucose breakdown is 6:1, then for root tip and non-root tip respiration rates of 5.76 and 2.16 μmol O_2 cm^{-1} root d^{-1} the corresponding usage of C in these regions, if glucose is used as the sole respiratory substrate, is 69 and 26 μg C cm^{-1} root d^{-1} respectively. In regions of the root where the formation of new biomass is minimal (6 to 7 cm behind the apex), the amount of soluble sugar C contained within the roots is 22 μg C cm^{-1} root (Fig. 5). Therefore, 83% of the total sugar pool present within the root is turned over per day. At the root tip where the usage of C is much higher due to the formation of new biomass, the partitioning of C partitioned into biomass production can be calculated at 94.3%, assuming that the ion uptake and maintenance C demand is uniform along the root length. In the production of new biomass at the root tip (0 to 1 cm), the amount of C incorporated into new dry weight is 89.9% compared to the CO_2 produced in its formation (respiration = 10.1%) (calculation assumes growth rate of 2 cm d^{-1} or 384 μg C d^{-1}; root density of 1.0, root mineral content of 4%, C content of 0.4% and root moisture content of 90%). If the soluble sugar pool at the root tip is 35 μg C cm^{-1} root (Fig. 5), the total turnover of soluble sugar C within the 0 to 1 cm root region per day is therefore between 14 to 15 times that of the total soluble sugar C pool.

Discussion

In most previous rhizosphere C studies it has been assumed that the flow of C occurs as a unidirectional flux, whereby C is lost irretrievably from the root into the soil (Curl and Trueglove, 1986; Whipps, 1990). Once in the soil it was presumed that the C would diffuse away from the root until it was captured and degraded by the soil's miciobial population, leading to microbial growth and hence the rhizosphere effect. This present study on sugars, and similar stud-

ies on amino acids (Jones and Darrah, 1994; Von Wiren et al., 1994) have now shown that C flow at the soil-root interface is bi-directional. From analysis of both the inhibitor studies and root concentrations it appears that the influx of sugars into maize roots occurs against the concentration gradient probably involving a H^+-ATPase dependent plasmalemma proton co-transporter. This is further supported by electrophysiological and kinetic studies on maize roots by Xia and Saglio (1938, 1990) and Kennedy (1977). In contrast, the efflux of sugars from maize roots appears to be due solely to the passive or facilitated diffusion of sugars down their concentration gradient. The experimental results also suggested that the rate of sugar efflux from the root was linearly correlated with internal root concentration, indicating that the rate of sugar leakage is directly proportional to the root solution concentration gradient. For a cytoplasm-soil solution glucose gradient (C_i - C_o) of 72 m*M* (from Fig. 5 assuming 1 cm^3 root = 197 cm root length), and a plasmalemma permeability coefficient (P) of 1.15×10^{-4} cm h^{-1} (Bresseleers et al., 1984 and references therein) the mean rate of passive glucose leakage into the soil (J) can be calculated from the equation:

$$J = AP(C_i - C_o)$$

If exudation is assumed to occur from the epidermis only (Surface area (A) = 0.37 $cm^2 cm^{-1}$ root), the rate of glucose loss can be estimated at 74 nmol glucose cm^{-1} root d^{-1} (5.3 μg C cm^{-1} root d^{-1}). If exudation is assumed to occur from both epidermal and cortical cells (A = 11.2 cm^2 cm^{-2} root), the rate of glucose efflux can be estimated at 2234 nmol glucose cm^{-1} root d^{-1} (161 μg C cm^{-1} root d^{-1}), assuming radial geometry and an apoplastic sugar concentration of 0 μM. These values therefore provide a minimum and maximum estimate of maize root glucose C losses. Comparison with model and experimental values found by Jonas and Darrah (1993) (efflux range = 6 to 59 μg sugar C cm^{-1} root d^{-1}), show a close agreement with these estimates providing further evidence for the passive nature of efflux. On analysis of the spatial distribution of sugars along maize roots it can therefore be deduced that efflux of sugars will occur from all areas of the root with maximum exudation rates observed in the 0–20 mm zone where the concentration of sugars is highest. If sugars are unloaded from the phloem by an apoplastic route (Lucas and Madore, 1988) the rates of efflux can be expected to be even higher at the root apices.

The efficiency of the root's mechanism for the recapture of sugars from both the apoplast and soil, requires that competition from the soil's microbial biomass is not overwhelming. Current estimates of root coverage by soil microorganisms varies from 2 to 15% depending on root zone and environmental conditions (Bowen and Rovira, 1973; Klein et al., 1990). Coody et al. (1986) showed that the affinity constant (K_m) far glucose uptake by soil microorganisms was $\simeq$350 μM, similar to that found for the high affinity glucose transport system of maize roots (800 μM). These values indicate that the transport capacity of both microorganisms and roots is similar.

The results indicate that C turnover and flow within the root is extremely dynamic with a rapid turnover of the soluble sugar pool each day in both growing and non-growing root regions. The results presented here and in Jones and Darrah (1994) indicate that gramineaceous roots are capable of taking up most sugars and amino acids from an exogenous solution against their concentration gradient. These results and the spatial data presented above indicate that the influx and efflux processes are inextricably linked both with respect to the solutes capable of transportation and also spatially and temporally (no temporal influx/efflux patterns were observed in any of the experiments). This, and a study by Jones and Darrah (1993) provide evidence that the plant can exert direct control over the levels of C accumulation in the rhizosphere. The obvious benefit of this is that levels of soluble C compounds in the rhizosphere can be reduced, thereby reducing both the colonizing potential and chemotaxis of deleterious bacteria and fungi towards the root. The C efficiency of the plant will also be increased.

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