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Glucose uptake by maize roots and its transformation in the rhizosphere

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Abstract

The flow of carbon from roots into the rhizosphere represents a significant C loss from plants. However, roots have the capacity to recapture low molecular weight C from soil although this is in direct competition with soil microorganisms. The aim of this study was to investigate the behaviour of glucose in rhizosphere and non-rhizosphere soil, the plant's potential to recapture sugars from soil and translocation and utilization of the recaptured sugars. In microcosms containing maize plants we injected ^{14}C-glucose into the rhizosphere and followed its uptake into plants, upward and downward transport in the plant and soil, evolution as $^{14}CO_2$ and incorporation into the soil microbial biomass. These fluxes were compared with non-rhizosphere soil. Glucose was rapidly mineralized in soil and the rate of turnover was significantly greater in the rhizosphere in comparison to non-rhizosphere soil. The amount of glucose captured by the maize plants was low (<10% of the total ^{14}C-glucose added) in comparison to that captured by the soil microbial biomass. Only small amounts of the ^{14}C-glucose were transported to the shoot (0.6% of the total). The degree of glucose capture by maize roots whilst in competition with soil microorganisms was similar to similar experiments performed for amino acids. We conclude that while plant roots can recapture low molecular weight C from the rhizosphere, intense competition from soil microorganisms may reduce the efficiency of this process.

Keywords: Competition; Carbon flow; Dissolved organic carbon; Low molecular weight organics; Root exudation; Rhizodeposition; Rhizosphere; Sugar

1. Introduction

Plants release a large amount of their photosynthetically fixed carbon into the soil either as CO_2 in root respiration or as soluble and insoluble C compounds during root turnover and exudation (Nguyen, 2003). In addition, large amounts of C can pass directly into the soil microbial community via transfer to symbionts (e.g. mycorrhizas; Jones et al., 2004a,b). Estimates of the amount of C lost in root exudation (rhizodeposition) typically range from 1 to 10% of a plant's net fixed C (Kuzyakov and Domanski, 2000; Nguyen, 2003). The magnitude of this flow has been shown to be dependent upon a wide range of biotic (e.g. herbivory, pathogen attack) and abiotic factors (e.g. temperature, soil physical structure, nutrient availability; Nguyen, 2003; Dakora and Phillips, 2002; Jones et al., 2004a). Although 200 or more individual compounds can be lost from plant roots into soil, root exudation is dominated by low molecular weight compounds such as sugars (e.g. glucose, sucrose), amino acids (e.g. glutamate, glycine) and organic acids (e.g. citrate, lactate; Farrar et al., 2003). Due to the complexity of the reactions of these compounds in soil their fate in soil remains poorly understood. After release of the exudates into the soil solution, they can be taken up and biodegraded by the soil microbial community, abiotically mineralized by soil minerals, leached from the soil profile, sorbed to the solid phase or taken up by plants. The relative importance of these individual fluxes remains poorly understood partially due to the interactions between these factors and the high degree of spatial heterogeneity in the rhizosphere (Jones and Edwards, 1999).

Previous work has shown that maize roots release most of their low molecular weight exudates by passive diffusion as a result of the high concentration gradient that exists between the cytoplasm (typically mM) and

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the soil solution (typically μM; Jones and Darrah, 1996). In the case of negatively charged exudates such as organic acid anions, exudation is further enhanced by the electrochemical potential gradient that is generated by the plasma membrane H^+-ATPase (Mühling et al., 1993; Jones et al., 2004a,b). In the case of neutrally charged sugars, such as glucose, we have shown that maize roots can recapture sugars previously lost in exudation (Jones and Darrah, 1992, 1993). Both at the molecular and physiological level this has been shown to be an active transport process mediated by proteins which can cotransport H^+ and sugars and which are driven by the protonmotive gradient created by the H^+-ATPase (Jones et al., 2004a,b). The uptake of sugars by maize roots shows similar Michaelis–Menten kinetic parameters (i.e. K_m, V_{max}) to those of the soil microbial community (Xia and Saglio, 1988; Coody et al., 1986). This would imply that an intense competition for sugars exists in the rhizosphere between the soil microbial community and plant roots (Hodge et al., 2000). However, there have been few direct studies investigating this aspect of rhizosphere C flow. Similar studies undertaken with amino acids in temperate soils have suggested that plant roots are poor competitors for amino acids in soil while others in arctic tundra environments have suggested the opposite view (Chapin et al., 1993; Owen and Jones, 2001; Bardgett et al., 2003). These results imply that the degree of competition may be very ecosystem dependent and that further studies are required to elucidate the factors regulating the competitive ability of both plants and soil microorganisms.

Another important factor of the competition between roots and microorganisms is spatial localization of low molecular weight organic substances. The roots can only compete for substances, which are located in the direct vicinity of the root surface. Due to interactions of most low molecular weight organic substances with soil organic matter, clay minerals or sesquioxides as well as microorganisms, the mass flow of these substances to the roots over distances beyond a few millimeters is of minor importance. Therefore, the uptake of organic substances by roots and competition with microorganisms can only be important in the rhizosphere. Consequently, studies investigating the uptake of organic compounds injected into non-rhizosphere soil may strongly underestimate root uptake and its competitive strength (Nasholm et al., 2000).

The aim of this study was to investigate the temporal and spatial dynamics of glucose in rhizosphere and non-rhizosphere soil. In addition, the partitioning of glucose taken up by maize plants was also investigated. Maize was chosen as a model plant as its rates of sugar exudation and transport are well documented while glucose was chosen as a model compound as it frequently dominates root exudation.

2. Materials and methods

2.1. Soils and sampling

Soil (Eutric Cambisol) was obtained from the University of Wales–Bangor Henfaes Agricultural Research Station located in Abergwyngregyn, Gwynedd, North Wales (53°14′N, 4°01′W). Soil samples were collected from the Ah horizon (5–20 cm; silty clay loam texture) of a lowland (15 m altitude) freely-draining, heavily sheep-grazed grassland which receives regular fertilization (120 kg N, 60 kg K and 10 kg P ha^{-1} y^{-1}) and supports a sward consisting predominantly of perennial ryegrass (*Lolium perenne* L.), clover (*Trifolium repens* L.) and crested dog's tail (*Cynosurus cristatus* L.). Maize for animal fodder is often planted in this soil type in a rotational cropping cycle directly after plowing in grassland. Soil was removed using a spade and stored in CO_2 permeable polypropylene bags for immediate transport back to the laboratory. In the laboratory, the soil was sieved (<5 mm) and then stored field-moist at 3 °C in the same bags. Earthworms, above-ground vegetation and large roots were removed by sieving. The pH of the soil was 5.7, total organic C was 53 g kg^{-1} and total *N* was 2.6 g kg^{-1}. Further properties of the soil are presented in Jones et al. (2004b).

2.2. Plant growth conditions and experimental system

Seeds of maize (*Zea mays* L. cv. 'Merit') were soaked for 24 h in aerated deionized water and then allowed to germinate on moistened filter paper at 20 °C. After 3 days, each plant had one main root axis approximately 1.5 cm in length, at which point the seedlings were placed into individual soil microcosms. Control microcosms contained soil but no plants.

The plant–soil microcosms were constructed from polyethylene tube as described in Owen and Jones (2001); Jones et al. (2005). Briefly, the microcosms were composed of a 20 cm long, 0.6 cm internal dia. main 'rhizotube' section connected to a 4 cm long, 1.8 cm dia. section, which was used to hold the seed (Fig. 1). The microcosms were filled with soil to a bulk density of 0.8 g cm^{-3}.

After the addition of seedlings, the microcosms were placed in a climate-controlled growth room (Sanyo-Gallenkamp, Fitotron PG660/C/RO/HQI, Loughborough, UK) with day/night rhythm of 20 °C, 70% relative humidity, photoperiod of 12 h and light intensity of 500 μmol photons m^{-2} s^{-1} PAR at canopy height. Carbon dioxide concentrations within the growth cabinets were maintained at 350 ppm by regular changes with external air. Microcosms were kept moist by the addition of water twice daily. Initially, the microcosms were watered with distilled water; however, starting on day 10, alongside the water 4 ml of full strength Long Ashton nutrient solution (Hewitt, 1966) was added daily to the microcosms.

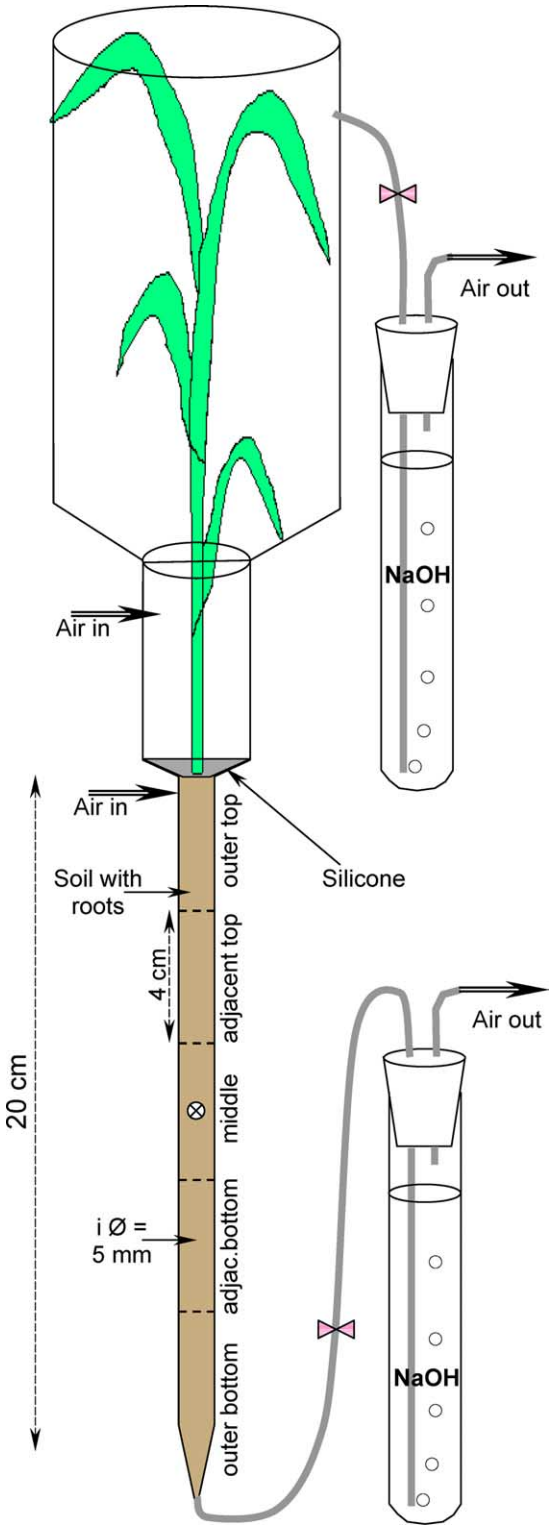

Fig. 1. Schematic representation of the maize rhizosphere microcosms into which ^{14}C-labelled glucose was injected. The ^{14}C-glucose was injected into the hole (⊗) in the middle soil section. The ^{14}C-glucose movement and incorporation into different root and soil sections and shoots was measured after different periods after the injection. The root/soil and shoot compartments were isolated by a silicone seal allowing separate measurements of $^{14}CO_2$ evolved from the shoots and root compartments by trapping in NaOH. The same microcosms were used for root-free soil.

When the roots and associated root hairs had completely occupied the microcosm making it essentially all rhizosphere soil (15 d after transplantation; shoots 12–15 cm long), the soil–root compartment was sealed with a 5 mm layer of non-phytotoxic silicon rubber paste (NG 3170; Thauer & Co., Dresden, Germany). This allowed the separate trapping of CO_2 evolved from the upper (shoot) and lower (root and soil) compartments (Fig. 1). 200 μl of a uniformly ^{14}C-labelled glucose solution (100 μM; 7.1 kBq ml^{-1}; Sigma Chemical Co., St Louis, MO) was then injected through a hole into the side of the middle of the microcosm and into the centre of the rhizosphere soil. The upper part of the microcosm containing the shoots was then sealed with a polypropylene chamber, which permitted photosynthesis but also allowed the trapping of CO_2 evolved from shoot respiration (Fig. 1).

2.3. Treatments

The experiment had three principal treatments, namely: (1) planted soil with 12 h photoperiod; (2) planted soil with a continuous 24 h photoperiod; and (3) unplanted soil with 12 h photoperiod.

2.4. Harvesting of the microcosms

In the subsequent 4 days after glucose injection into the microcosms, CO_2 efflux from the upper shoot compartment (i.e. shoot respiration) and from the lower soil–root compartment (i.e. root and microbial respiration) were trapped separately in two subsequent 1 M NaOH traps (only one NaOH trap for shoots and for soil–root compartment is shown on Fig. 1 for simplicity) by pumping the air by membrane pumps (50 mL min^{-1}). In addition, during the 4 day ^{14}C chase period, the shoot and soil–root compartments were destructively harvested eight times using replicate microcosms. The soil–root compartment of each microcosm was separated into five zones, each 4 cm in length as shown in Fig. 1. These consisted of one central part, into which the glucose was injected, two adjacent parts (above and below the central part), and two outer parts (above and below the adjacent parts). After separation, the microcosm parts were immediately frozen at −20 °C. In each microcosm component part the amount of ^{14}C and total carbon (C_t) contained within the roots, dissolved organic carbon (DOC), and soil was determined. Briefly, frozen soil–root compartments (1.8 g) were shaken for 10 s with 3 ml of 0.05 M $CaCl_2$. The $CaCl_2$ solution was used to reduce the amount of organic-mineral colloids present in the DOC solution obtained. After shaking, the roots were recovered with tweezers. The roots were additionally shaken for 10 s with 3 ml of distilled water to remove the remaining soil particles and the roots were subsequently dried at 80 °C overnight.

After removal of the roots, the remaining soil was shaken with the $CaCl_2$ solution for 1 h and then centrifuged for

10 min at 2500 rpm. The supernatant recovered was the DOC fraction. The DOC solution obtained was clear and contained no colloids. The remaining soil was dried at 80 °C and stored before the determination of total ^{14}C radioactivity.

The ^{14}C content of the shoots, roots and soil was determined using a OX400 Biological Oxidiser (Harvey Instruments Corp., Hillsdale, NJ) and liquid scintillation counting (Wallac 1409; EG&G Ltd, Milton Keynes, UK). ^{14}C in DOC was determined by liquid scintillation counting using Optiphase HiSafe 3 liquid scintillation cocktail (EG&G Ltd). Total dissolved organic C in soil solution was determined with a Shimadzu TOCV-TNM1 analyzer (Shimadzu Corp., Kyoto, Japan).

2.5. Glucose sorption

Glucose sorption to the solid phase was determined by shaking 1 g of soil with 2 ml of a 100 μM glucose solution (0.17 kBq ml^{-1}) for 15, 30 or 60 min on a reciprocating shaker at 200 rpm. The soil suspensions were then centrifuged (14,000*g*, 5 min) and the amount of ^{14}C remaining in solution determined by liquid scintillation counting as described above. To determine whether microbial activity interfered with the sorption experiment $HgCl_2$ (50 mM) or Na-azide (50 mM) was included in the glucose solution. Additionally, the soil was either autoclaved (121 °C, 103 kPa, 30 min) or heated (80 °C, 3 h) immediately before the addition of the glucose solution.

2.6. Statistical analysis

All results are presented as percentage of ^{14}C input (^{14}C added as glucose). The sum of ^{14}C recovered in all compartments of each pot was always higher than 90% of ^{14}C input. The main experiment was conducted with four replications. In retrospect, as no significant differences were observed for any parameters between the planted treatments exposed to either a 12 or 24 h photoperiod (Section 3), both planted treatments were pooled and considered as replicates. Statistical analysis (*t*-tests, ANOVA) was undertaken with Statistica (StatSoft Inc., 2001).

3. Results

3.1. Glucose mineralization in the rhizosphere and root-free soil

Glucose was very rapidly mineralized to CO_2 after injection into the rhizosphere (Fig. 2). The rate of glucose mineralization was significantly greater in the root-filled (rhizosphere) microcosms in comparison to the root-free (non-rhizosphere) microcosms ($P<0.05$). Within the first hour after injection, 7% of the ^{14}C-labelled glucose had been recovered as $^{14}CO_2$ while only 2.3% was recovered as $^{14}CO_2$ in the unplanted microcosms (Fig. 2, top). Assuming the mineralization kinetics follow a first order decay model, the rate constant were calculated to be 0.24 ± 0.03 and $0.13\pm0.02\ h^{-1}$ for the rhizosphere and root-free soil, respectively. After this initial difference, which lasted for 24 h, generally the rate of $^{14}CO_2$ production was not significantly different between planted and unplanted microcosms ($P>0.05$). At the end of the experiment (96 h) the total amount of $^{14}CO_2$ recovered was approximately twofold higher in the planted microcosms in comparison to the unplanted microcosms (Fig. 2, bottom). Although the rate of $^{14}CO_2$ evolution was very low after 96 h a maximum of 30% of the total ^{14}C added was recovered as root–soil respiration indicating that a large proportion was immobilized in the plant or soil. The length of the maize photoperiod had no significant effect on the rate of glucose mineralization after addition to the rhizosphere ($P>0.05$; Fig. 2).

3.2. Glucose recovery in soil and DOC

The main part of the ^{14}C-glucose that was not mineralized to $^{14}CO_2$ during the first four days was recovered from the soil and was assumed to be immobilized in the soil microbial biomass (Fig. 3) or in DOC (see below). The amount of ^{14}C present in the soil clearly reflected the amount of glucose mineralized to CO_2. In the non-rhizosphere microcosms approximately 15% more ^{14}C was recovered from the soil in comparison to the planted rhizosphere soil ($P<0.05$). Although $98\pm2\%$ of the ^{14}C-glucose could be recovered from the soil immediately after addition (in sterilized controls, see Fig. 4), this had dropped to between 45 and 58% after 1 h in the microcosms. After this period, the amount of ^{14}C recovered from the soil was relatively stable over the 96 h experimental period. This finding is also consistent with an initially rapid production of $^{14}CO_2$ and the biotic immobilization of the substrate (Jones, 1999). This is supported by sorption experiments which showed that in microcosm soil sterilized either by temperature (autoclaving or heating to 80 °C) or the addition of chemical toxins (Na-azide, $HgCl_2$) no significant sorption of glucose to the solid phase occurred (Fig. 4). In contrast, in the unsterilized soil, ^{14}C-glucose was rapidly depleted from the solution phase with approximately 90% of the glucose removed from solution within 1 h of addition.

Although the greatest amounts of ^{14}C were recovered from the zone of soil into which the ^{14}C glucose was initially injected, some ^{14}C was also recovered above and below this zone as DOC (Fig. 5). Generally, this movement of ^{14}C was significantly greater in the planted versus the unplanted microcosms. Consequently, the ^{14}C recovered in the rhizosphere soil as DOC was always approximately three to sixfold higher than in the unplanted soil. This provides evidence that a proportion of the glucose was taken

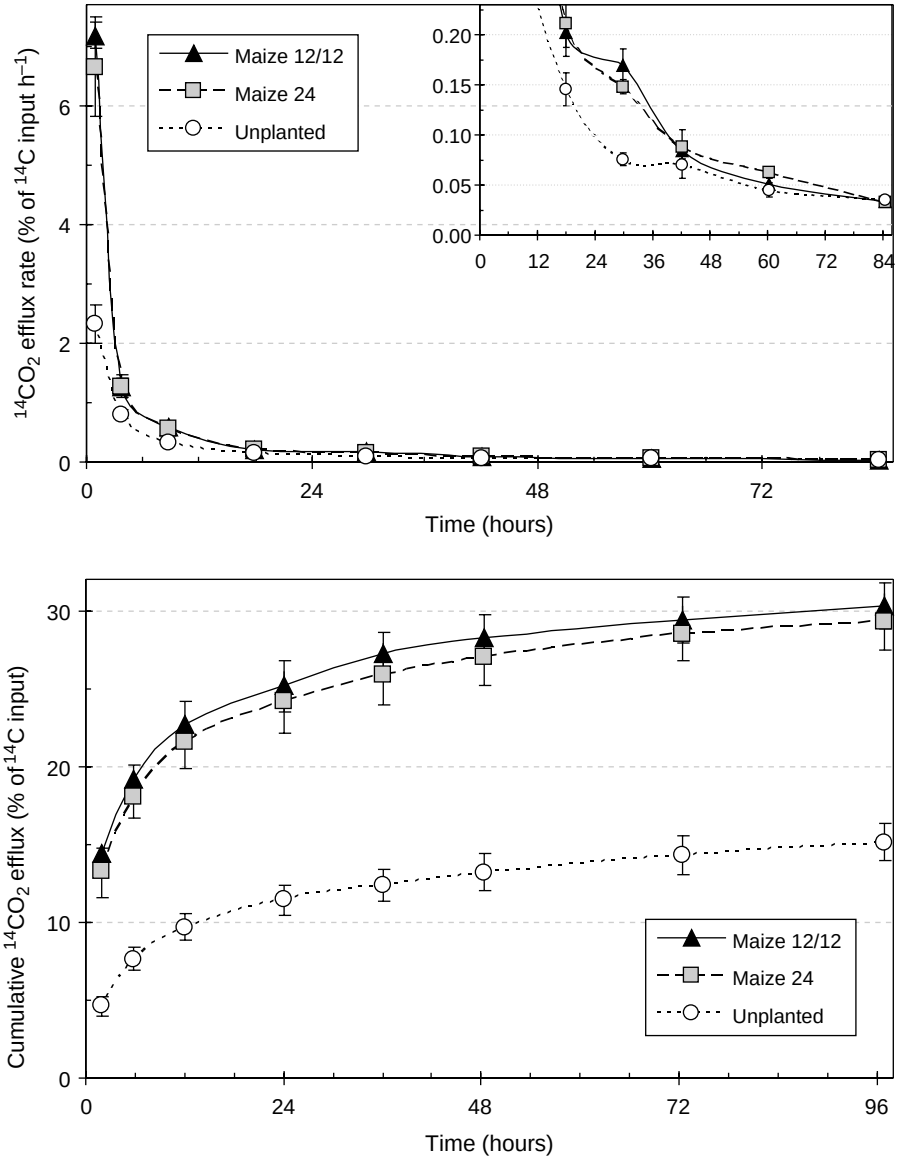

Fig. 2. Mineralization of ^{14}C-labelled glucose after injection into the soil-filled microcosms containing either (a) maize plants with differing photoperiods, or (b) no plants. The top panel shows the rate of glucose mineralization to $^{14}CO_2$ and the bottom panel shows the cumulative evolution of $^{14}CO_2$ from the microcosms. The two photoperiods were 12/12 h dark/light or 24 h continuous light. The inset panel shows the $^{14}CO_2$ efflux rates after 12 h at a higher *y*-axis resolution. Values represent means ± SEM ($n=4$).

up into the roots (see below) and transported to upper and lower root parts where loss as exudation may have occurred.

A difference in the dynamics of ^{14}C recovered as DOC in the soil zones was also apparent between the planted and unplanted microcosms. In the root free soil, after an initial decrease of DOC concentration during the first 12 h, it remains nearly constant until the end of the experiment. In the rhizosphere soil, a similar temporal pattern of DOC was observed for the middle soil zone layer only, where the glucose was injected directly. In the soil zones above and below the point of injection, it took 1–2 d to reach a maximal concentration of ^{14}C-DOC after which a decrease occurred (Fig. 5). This initial increase and subsequent decrease of ^{14}C in DOC in the planted microcosms suggests that some time is necessary for uptake of the glucose, its transportation to the other root parts and subsequent release into the rhizosphere.

3.3. Glucose uptake and distribution in roots

We readily acknowledge that the method used here for the physical separation of roots from soil may underestimate the uptake of glucose taken into the root, due to possible damage and loss of ^{14}C label from the roots during washing. This effect could be particularly pronounced during the first sampling events when glucose will be present predominantly in the root's soluble pool (Jones and Darrah, 1996). At the end of the experiment (96 h) when most of the ^{14}C

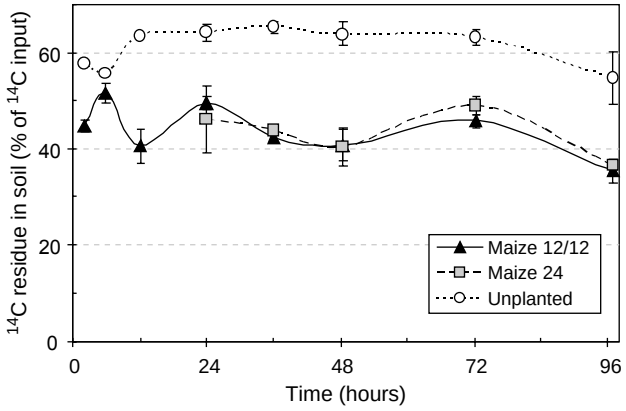

Fig. 3. Amount of ^{14}C remaining in the soil after the injection of ^{14}C-glucose into the planted or unplanted microcosms. Only data for the central microcosm part, in which the glucose was injected, is presented after removal of roots and extraction of DOC. Values represent means ± SEM (n = 4).

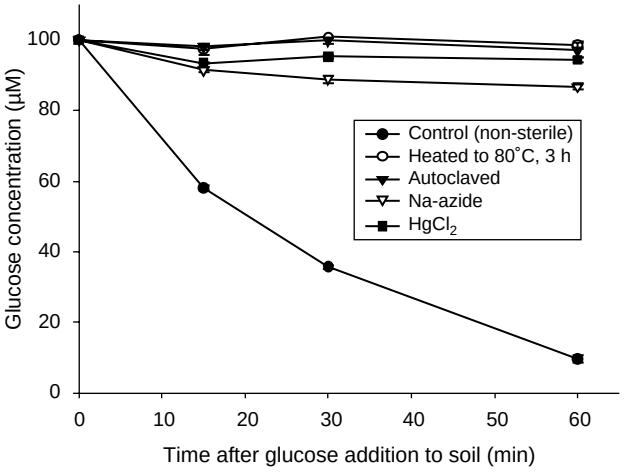

Fig. 4. Depletion of ^{14}C-labelled glucose from soil either before (non-sterile control) or after thermal treatment (80 °C or autoclaving) or the addition of chemical toxins ($HgCl_2$ and Na-azide). Values represent means ± SEM (n = 3).

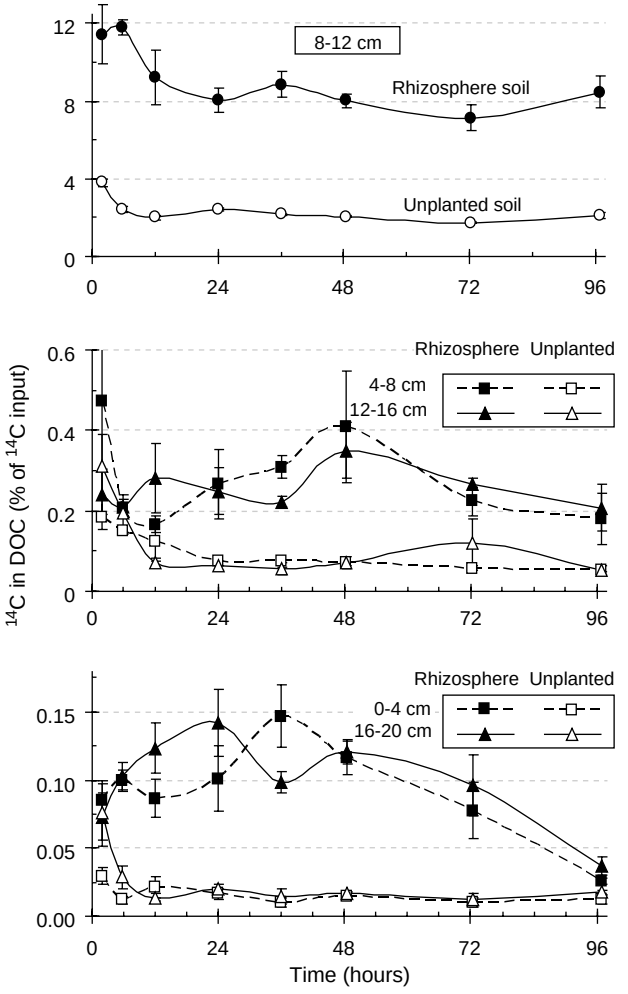

Fig. 5. Dynamics of soluble ^{14}C (DOC) recovered from different parts of the soil-filled microcosms following the injection of ^{14}C-glucose. The parts of the microcosm are: 8–12 cm, central part; 4–8 and 12–16 cm: parts adjacent the central parts above and below, respectively; 0–4 and 16–20 cm above and below outer parts, respectively. DOC of planted soil is presented as filled symbols; DOC of unplanted soil is presented as open symbols. Note the different y-axis scale on the figures. Values represent means ± SEM (n = 4).

should be incorporated into insoluble residues in the root, however, it is expected that this washing-induced loss of ^{14}C label will be minimal.

At the first sampling event (2 h after glucose addition), 2.2% of the ^{14}C was recovered in the middle part of the microcosm adjacent to where the ^{14}C-glucose had been injected (Fig. 6). After this initial rapid incorporation of glucose into the root, the ^{14}C concentration in the middle part of the root remained at a near constant level until the end of experiment at 96 h. The absence of further ^{14}C incorporation into the middle root section corresponds to the short half-life of free glucose in soil solution (Fig. 4).

The ^{14}C dynamics in other root zones were different from the middle part of the microcosms where the injection occurred. In the root zones immediately adjacent to the middle root part, small amounts of the ^{14}C were recovered either above (0.09% of total ^{14}C) or below (0.05% of the total ^{14}C) after 2 h. These values increased until day three (0.36 ± 0.06 and 0.23 ± 0.08%, respectively) and then decreased. The decrease was connected with a release of ^{14}C into the rhizosphere as DOC (see above) or as CO_2 from root respiration (the two CO_2 sources cannot be separated in our system). After 2 d both loss processes (exudation and root respiration) were higher than the rate of ^{14}C uptake into the roots. It is noticeable that the root zones above the central injection zone possessed a significantly higher ^{14}C content than those below it ($P < 0.05$) (Fig. 6).

3.4. ^{14}C allocation in shoots and shoot respiration

Small amounts of the total ^{14}C added to the microcosms (0.2–0.9%) were recovered in the maize shoots (Fig. 7). These amounts were about 3–9 times less than the total

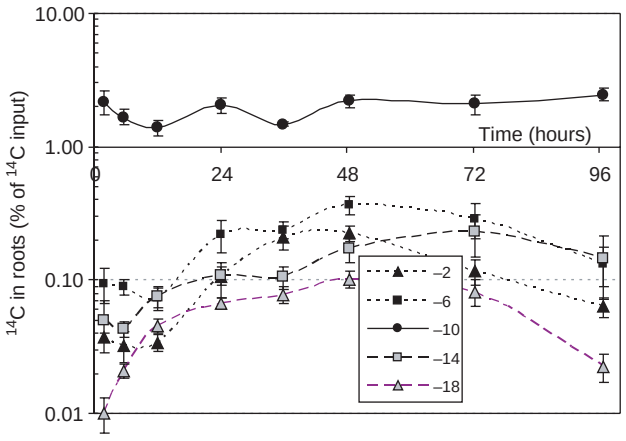

Fig. 6. Dynamics of ^{14}C from glucose (in % of ^{14}C input) recovered in different parts of roots: 0–4, 4–8, 8–12, 12–16, and 16–20 cm. Glucose was injected into the soil at a depth of 10 cm (the centre of the 8–12 cm part). Note the logarithmic *y*-axis scale. Values represent means ± SEM (n = 4).

amount of ^{14}C recovered in the roots. After the first sampling, the ^{14}C activity in the shoots increased until 48 h after which it declined until the end of the experiment. This decrease during the last 48 h is associated with two processes: respiration of the glucose or its labelled transformation products by the shoots, or its re-translocation back to the roots with the main photosynthetic stream. Measuring the shoot respiration, we found only very minor ^{14}C activity in the CO_2 trapped from the shoots. Over the whole 4 d experimental period, only 0.08 ± 0.02% of the ^{14}C was recovered as $^{14}CO_2$ from the shoots in the 12/12 day/night photoperiod treatment and 0.06 ± 0.01% of the total ^{14}C added in the 24 h continuous illumination treatment. These amounts are not sufficient to explain the decrease of ^{14}C in the shoots during the last 48 h of the experiment, in which approximately 0.5% of the total ^{14}C was lost from the shoots (Fig. 7).

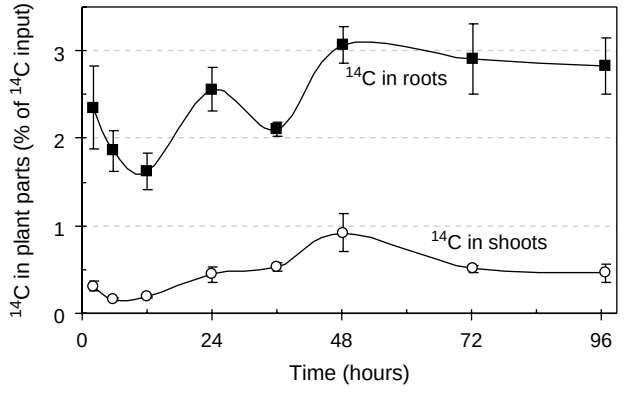

Fig. 7. Total amount of ^{14}C recovered in the shoots and roots of maize plants after the injection of ^{14}C-labelled glucose into the soil. Values represent the amount of ^{14}C recovered as a percentage of the total ^{14}C-glucose injected into the microcosms. Values represent means ± SEM (n = 4).

4. Discussion

4.1. Glucose concentrations in the rhizosphere

Our experiments were designed to investigate the competition between soil microorganisms and plant roots for labile C in the rhizosphere arising from either root exudation or the breakdown of soil organic matter. The degree of competition can be expected to be dependent to a large extent upon the spatial location of the sources and sinks for the labile C, in this case glucose, and their relative concentrations.

The amount of glucose added to the rhizosphere was chosen to reflect the typical concentration of free glucose observed in the soil solution of this Eutric Cambisol (50–100 μM). The actual spatial concentration profile of glucose that exists in the maize rhizosphere within our microcosms, however, remains unknown. Taking a theoretical approach, Darrah (1991a) predicted that the glucose concentration in the rhizosphere in response to cereal root exudation would be in the region of 50–500 μM. Assuming a constant exudation rate for glucose from maize roots (74 nmol cm^{-1} d^{-1}; Jones and Darrah, 1996), rhizosphere radius of 2 mm, and soil water content of 30%, we calculate that the average concentration of glucose in the soil solution of the maize rhizosphere will be in the region of 100–500 μM after a few hours of exudation (assuming no microbial degradation). Due to the lack of glucose sorption to the solid phase and its rapid rate of diffusion in soil, the concentration profile away from the root is unlikely to be steep with diffusive movement across the entire extent of the rhizosphere likely within a few hours (Darrah, 1991b). However, if microbial decomposition of glucose occurs the concentration gradient will be much steeper (Kuzyakov et al., 2003). Although the exact spatial and temporal dynamics of glucose exudation from roots in soil is poorly understood, we think that the concentrations employed here will still allow root-microbial competition to be reliably assessed. This assumption is based upon our knowledge of the Michaelis–Menten kinetic parameters (K_m and V_{max}) for glucose uptake by both soil microorganisms and plant roots. The affinity constant (K_m) for microbial glucose transporters typically ranges from 300 to 1000 μM while the K_m value for the high affinity transport system of roots ranges from 800 to 1500 μM (Coody et al., 1986; Xia and Saglio, 1988; Jones and Darrah, data not presented). Therefore, the amount of glucose we added to the microcosms lies well within the concentration range where competition should remain largely independent of initial concentration (i.e. where Michaelis–Menten kinetics approximates a first order kinetic model). This is supported by data presented in Jones et al. (2005) where the level of competition for amino acids between soil microorganisms and plant roots remained concentration independent until the uptake capacity of the microbial community became saturated.

4.2. Root–soil competition for glucose in the rhizosphere

The uptake of sugars by roots from a range of crop plants grown in sterile hydroponic solutions is well documented (Xia and Saglio, 1988; Jones and Darrah, 1993; Vucinic and Vuletic, 1995; Sacchi et al., 2000; Stubbs et al., 2004). Further, the addition of sucrose to agar is regularly used as a mechanism for enhancing the growth of *Arabidopsis thaliana* plants in the laboratory (Sherson et al., 2000). In addition, in *Arabidopsis* the external supply of sugar to the roots has been shown to modulate adventitious rooting (Takahashi et al., 2003). The purpose of this constitutively expressed sugar active transport system in roots, however, remains unclear although it has been shown to influence ion uptake and developmental processes (Quintero et al., 2001; Sacchi et al., 2000). Our results suggest that plants were relatively poor competitors for glucose present in the soil. A similar result has also been reported for amino acids in the rhizosphere (Owen and Jones, 2001; Bardgett et al., 2003). We have previously hypothesized that the function of these transporters is to capture root exudates, which are passively lost into the soil to reduce microbial proliferation around the roots (Jones and Darrah, 1996). Based upon the results presented here it is clear that capture from the soil probably only constitutes a small amount of the C required by the root. The respiratory demand of a maize root requires a supply of sugar ranging from 0.2 to 1.0 μmol glucose cm^{-1} d^{-1} (Jones and Darrah, 1996). Our results showed that approximately 3.5% of the ^{14}C-glucose added to the microcosms was recovered in the plant. Although we could not separate root and microbial respiration in our experiments, previous experiments have indicated that approximately 45% of the glucose-C taken up by roots is subsequently respired as $^{14}CO_2$ (Jones and Darrah, 1992). Taking this into account we conclude that approximately 8% of the added glucose was captured by the plant. Based upon the likely partitioning of glucose in the root soluble (30% of total) and insoluble pools (70% of total; Jones and Darrah, 1992) it is also likely that only a small proportion of the ^{14}C was lost from the roots during washing. Taking this washing loss into account and assuming a maximal uptake of 10% of the added glucose by the plant, this corresponded to less than 1% of the respiratory C requirement of a root. This result also suggests that the capture of C from decomposing organic matter in soil is unlikely to have a significant impact on the plant's C budget unless the plant is non-photosynthetic (e.g. *Orobanche minor*; Taylor et al., 2004).

During root exudation, glucose will first be lost from the cytoplasm into the space between the plasma membrane and the cell wall, and in the case of the cortex it will then pass into the apoplast. In both these situations, the microbial population is low and the root is likely to be best placed to recapture this glucose. Our experiments do not adequately reflect this situation and further experiments would need to be designed to explicitly test root capture efficiency under these conditions. Unlike a true rhizosphere situation where the glucose concentration is maximal at the root surface and declines with distance away from the root, we injected glucose uniformly throughout the rhizosphere. We hypothesize that this would favour microbial capture. While out results clearly demonstrate that roots can capture glucose from soil it is probably an underestimate of their true potential to capture root exudates.

The root and soil parts located above the part in which the glucose was injected recovered higher ^{14}C amounts than the respective below parts. This is clear evidence that glucose was preferably transported with the main upward water stream. This upward directed transport of glucose was about two times higher than the downward transport.

4.3. Glucose dynamics in the rhizosphere

Previous work has shown that the time taken for photosynthetically fixed C to reach the soil via exudation is small (within 1 h; Cheng et al., 1993; Kuzyakov et al., 2001; Dilkes et al., 2004). However, these very short periods are mainly responsible for the first appearance of assimilated C in the rhizosphere of grasses. As shown in pulse labelling experiments, the maximum of appearance of assimilates by grasses typically occurred about 12 h after assimilation (Kuzyakov et al., 2001). This period is much longer for trees and can be up to 4–6 d (Ekblad and Högberg, 2001). Our results suggest that once in the soil the exuded glucose will also be processed rapidly by the soil microbial community. Taken together these findings indicate that the microbial community will respond quickly to changes in the physiological status of the above ground plant parts (i.e. within hours). This can lead to the diurnal dynamics not only of root-derived CO_2 efflux from the soil (Kim and Verma, 1992; Oberbauer et al., 1992), but also to the diurnal dynamics of root-induced changes of SOM decomposition (Kuzyakov and Cheng, 2001).

In these experiments, we tracked ^{14}C rather than glucose directly. Therefore, some of the ^{14}C measurements may reflect glucose transformation products. This is particularly the case for the ^{14}C-DOC where this may reflect C that has been taken up by plants and microorganisms, metabolized, and then released back into solution.

The rate of glucose mineralization was significantly greater in the rhizosphere in comparison to the unplanted soil. While this may reflect an increased microbial activity in the rhizosphere soil (Kuzyakov, 2002), it may also indicate differential partitioning of glucose-C into catabolic and anabolic processes in the two treatments. As no measurements of microbial community structure or activity were undertaken in our microcosms the contribution of these factors to the enhanced mineralization remains unknown but warrants further study.

4.4. Conclusions

While plant roots have been shown many times to actively take up simple sugars from an external solution, this is the first study that demonstrates this phenomenon in a rhizosphere soil context. However, our study shows that the rhizosphere microbial community are highly effective in competing for this resource.

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References

Bardgett, R.D., Streeter, T.C., Bol, R., 2003. Soil microbes compete effectively with plants for organic-nitrogen inputs to temperate grasslands. Ecology 84, 1277–1287.

Chapin, F.S., Moilanen, L., Kielland, K., 1993. Preferential use of organic nitrogen for growth by a nonmycorrhizal arctic sedge. Nature 361, 150–153.

Cheng, W., Coleman, D.C., Carroll, C.R., Hoffman, C.A., 1993. In situ measurement of root respiration and soluble C concentrations in the rhizosphere. Soil Biology & Biochemistry 25, 1189–1196.

Coody, P.N., Sommers, L.E., Nelson, D.W., 1986. Kinetics of glucose-uptake by soil-microorganisms. Soil Biology & Biochemistry 18, 283–289.

Dakora, F.D., Phillips, D.A., 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant and Soil 245, 35–47.

Darrah, P.R., 1991a. Models of the rhizosphere. 1. Microbial-population dynamics around a root releasing soluble and insoluble carbon. Plant and Soil 133, 187–199.

Darrah, P.R., 1991b. Measuring the diffusion-coefficient of rhizosphere exudates in soil. 1. The diffusion of non-sorbing compounds. Journal of Soil Science 42, 413–420.

Dilkes, N.B., Jones, D.L., Farrar, J., 2004. Temporal dynamics of carbon partitioning and rhizodeposition in wheat. Plant Physiology 134, 706–715.

Ekblad, A., Högberg, P., 2001. Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. Oecologia 127, 305–308.

Farrar, J., Hawes, M., Jones, D.L., Lindow, S., 2003. How roots control the flux of carbon to the rhizosphere. Ecology 84, 827–837.

Hewitt, E.J., 1966. Sand and water culture methods used in studies of plant nutrition, Technical communication no. 22. Commonwealth Bureau of Horticultural and Plantation Crops, East Malling, Kent, UK.

Hodge, A., Robinson, D., Fitter, A., 2000. Are microorganisms more effective than plants at competing for nitrogen? Trends in Plant Science 5, 304–308.

Jones, D.L., 1999. Amino acid biodegradation and its potential effects on organic nitrogen capture by plants. Soil Biology & Biochemistry 31, 613–622.

Jones, D.L., Darrah, P.R., 1992. Resorption of organic-components by roots of Zea mays L. and its consequences in the rhizosphere. 1. Resorption of ^{14}C labeled glucose, mannose and citric-acid. Plant and Soil 143, 259–266.

Jones, D.L., Darrah, P.R., 1993. Re-sorption of organic-compounds by roots of Zea mays L. and its consequences in the rhizosphere. 2. Experimental and model evidence for simultaneous exudation and re-sorption of soluble C compounds. Plant and Soil 153, 47–59.

Jones, D.L., Darrah, P.R., 1996. Re-sorption of organic compounds by roots of Zea mays L and its consequences in the rhizosphere. 3. Characteristics of sugar influx and efflux. Plant and Soil 178, 153–160.

Jones, D.L., Edwards, A.C., 1999. Influence of sorption on the biological utilization of two simple carbon substrates. Soil Biology & Biochemistry 30, 1895–1902.

Jones, D.L., Hodge, A., Kuzyakov, Y., 2004a. Plant and mycorrhizal regulation of rhizodeposition. New Phytologist 163, 459–480.

Jones, D.L., Shannon, D., Murphy, D.V., Farrar, J., 2004b. Role of dissolved organic nitrogen (DON) in soil N cycling in grassland soils. Soil Biology & Biochemistry 36, 749–756.

Jones, D.L., Shannon, D., Junvee-Fortune, T., Farrar, J., 2005. Plant capture of free amino acids is maximized under high soil amino acid concentrations. Soil Biology & Biochemistry 37, 179–181.

Kim, J., Verma, S.B., 1992. Soil surface CO_2 flux in a Minnesota peatland. Biogeochemistry 18, 37–51.

Kuzyakov, Y., 2002. Review: factors affecting rhizosphere priming effects. Journal of Plant Nutrition and Soil Science 165, 382–396.

Kuzyakov, Y., Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology & Biochemistry 33, 1915–1925.

Kuzyakov, Y., Domanski, G., 2000. Carbon input by plants into the soil. Review. Journal of Plant Nutrition and Soil Science 163, 421–431.

Kuzyakov, Y., Ehrensberger, H., Stahr, K., 2001. Carbon partitioning and below-ground translocation by *Lolium perenne*. Soil Biology & Biochemistry 33, 61–74.

Kuzyakov, Y., Raskatov, A.V., Kaupenjohann, M., 2003. Turnover and distribution of root exudates of Zea mays. Plant and Soil 254, 317–327.

Mühling, K.H., Schubert, S., Mengel, K., 1993. Mechanism of sugar retention by roots of intact maize and field bean-plants. Plant and Soil 156, 99–102.

Nasholm, T., Huss-Danell, K., Hogberg, P., 2000. Uptake of organic nitrogen in the field by four agriculturally important plant species. Ecology 81, 1155–1161.

Nguyen, C., 2003. Rhizodeposition of organic C by plants: mechanisms and controls. Agronomie 23, 375–396.

Oberbauer, S.F., Gillespie, C.T., Cheng, W., Gebauer, R., Serra, A.S., Tenhunen, J.D., 1992. Environmental effects on CO_2 efflux from riparian tundra in the northern foothills of the Brooks Range, Alaska, USA. Oecologia 92, 568–577.

Owen, A.G., Jones, D.L., 2001. Competition for amino acids between wheat roots and rhizosphere microorganisms and the role of amino acids in plant N acquisition. Soil Biology & Biochemistry 33, 651–657.

Quintero, J.M., Molina, R., Fournier, J.M., Benlloch, M., Ramos, J., 2001. Glucose-induced activation of rubidium transport and water flux in sunflower root systems. Journal of Experimental Botany 52, 99–104.

Sacchi, G.A., Abruzzese, A., Lucchini, G., Fiorani, F., Cocucci, S., 2000. Efflux and active re-absorption of glucose in roots of cotton plants grown under saline conditions. Plant and Soil 220, 1–11.

Sherson, S.M., Hemmann, G., Wallace, G., Forbes, S., Germain, V., Stadler, R., Bechtold, N., Sauer, N., Smith, S.M., 2000. Monosaccharide/proton symporter AtSTP1 plays a major role in uptake and response of Arabidopsis seeds and seedlings to sugars. Plant Journal 24, 849–857.

StatSoft Inc., 2001. STATISTICA for Windows. Tulsa, OK.

Stubbs, V.E.C., Standing, D., Knox, O.G.G., Killham, K., Bengough, A.G., Griffiths, B., 2004. Root border cells take up and release glucose-C. Annals of Botany 93, 221–224.

Takahashi, F., Sato-Nara, K., Kobayashi, K., Suzuki, M., Suzuki, H., 2003. Sugar-induced adventitious roots in Arabidopsis seedlings. Journal of Plant Research 116, 83–91.

Taylor, D.L., Bruns, T.D., Hodges, S.A., 2004. Evidence for mycorrhizal races in a cheating orchid. Proceedings of the Royal Society of London Series B-Biological Sciences 271, 35–43.

Vucinic, Z., Vuletic, M., 1995. The effect of addition of sucrose on the energy status and the trans-root electrical potential difference of excised maize roots. Plant and Cell Physiology 36, 45–52.

Xia, J.H., Saglio, P.H., 1988. Characterization of the hexose-transport system in maize root-tips. Plant Physiology 88, 1015–1020.