

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 ¹⁴C-glucose into the rhizosphere and followed its uptake into plants, upward and downward transport in the plant and soil, evolution as ¹⁴CO₂ 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 ¹⁴C-glucose added) in comparison to that captured by the soil microbial biomass. Only small amounts of the ¹⁴C-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.

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1. Introduction

Plants release a large amount of their photosynthetically fixed carbon into the soil either as CO₂ 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 proton-motive 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 ($53^{\circ}14'N$, $4^{\circ}01'W$). 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 $10 \text{ kg P ha}^{-1} \text{ y}^{-1}$) 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 ($<5 \text{ mm}$) 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 $500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ 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.

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