Plant Soil (2009) 321:5–33
DOI 10.1007/s11104-009-9925-0

REVIEW ARTICLE

Carbon flow in the rhizosphere: carbon trading at the soil–root interface

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Received: 30 July 2008 / Accepted: 4 February 2009 / Published online: 25 February 2009
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Abstract The loss of organic and inorganic carbon from roots into soil underpins nearly all the major changes that occur in the rhizosphere. In this review we explore the mechanistic basis of organic carbon and nitrogen flow in the rhizosphere. It is clear that C and N flow in the rhizosphere is extremely complex, being highly plant and environment dependent and varying both spatially and temporally along the root. Consequently, the amount and type of rhizodeposits (e.g. exudates, border cells, mucilage) remains highly context specific. This has severely limited our capacity to quantify and model the amount of rhizodeposition in ecosystem processes such as C sequestration and nutrient acquisition. It is now evident that C and N flow at the soil–root interface is bidirectional with C and N being lost from roots and taken up from the soil simultaneously. Here we present four alternative hypotheses to explain why high and low molecular weight organic compounds are actively cycled in the rhizosphere. These include: (1) indirect, fortuitous root exudate recapture as part of the root's C and N distribution network, (2) direct re-uptake to enhance the plant's C efficiency and to reduce rhizosphere microbial growth and pathogen attack, (3) direct uptake to recapture organic nutrients released from soil organic matter, and (4) for inter-root and root–microbial signal exchange. Due to severe flaws in the interpretation of commonly used isotopic labelling techniques, there is still great uncertainty surrounding the importance of these individual fluxes in the rhizosphere. Due to the importance of rhizodeposition in regulating ecosystem functioning, it is critical that future research focuses on resolving the quantitative importance of the different C and N fluxes operating in the rhizosphere and the ways in which these vary spatially and temporally.

Keywords Carbon cycling · Nitrogen cycling · Mycorrhizas · Organic matter · Review · Rhizodeposition · Root processes · Signal transduction

Responsible Editor: Philippe Hinsinger.

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Introduction

For over a century it has been established that plants can dramatically modify their soil environment giving rise to the so called rhizosphere effect (Clark 1949;

Rovira 1965; Whipps 2001). Although the initial trigger of this rhizosphere effect was not identified, subsequent research has shown that it is largely induced by the release of carbon (C) from roots into the surrounding soil. Although roots can release large amounts of inorganic C which may directly affect the biogeochemistry of the soil (Cheng et al. 1993; Hinsinger 2001; Hinsinger et al. 2009), it is the release of organic carbon that produces the most dramatic changes in the physical, biological and chemical nature of the soil. In its broadest sense, this release of organic C is often termed rhizodeposition (Jones et al. 2004). The term rhizodeposition includes a wide range of processes by which C enters the soil including: (1) root cap and border cell loss, (2) death and lysis of root cells (cortex, root hairs etc), (3) flow of C to root-associated symbionts living in the soil (e.g. mycorrhizas), (4) gaseous losses, (5) leakage of solutes from living cells (root exudates), and (5) insoluble polymer secretion from living cells (mucilage; Fig. 1). Although these loss pathways can be clearly differentiated between at a conceptual level it is often extremely difficult at the experimental level to discriminate between them in both space and time. Consequently, while individual studies have shown that these can all occur, probably simultaneously in the same plant root system, it is almost impossible to rank the relative importance of each process. Further, as we understand more about the mechanisms of C flow in both soil and roots we find that many of the published results are severely biased by the experimental system in which individual factors or processes were examined (Jones and Darrah 1993; Meharg 1994; Kuzyakov 2006). This has left the literature on rhizosphere C flow awash with studies which may bear no relationship to real world events, particularly those performed in the absence of soil. Despite this, however, it is clearly apparent that our incremental approach to understanding C flow is paying dividends from both a commercial and environmental perspective. Firstly, from a commercial perspective it is clear that root C excretions can be useful for the non-destructive production of high value pharmaceuticals, pigments and flavours for use in the medical and cosmetic industries (Oksman-Caldentey and Inze 2004). In these applications, roots are typically transformed with *Agrobacterium rhizogenes* which induces hairy root disease. The neoplastic (cancerous) transformed roots are genetically stable and can grow

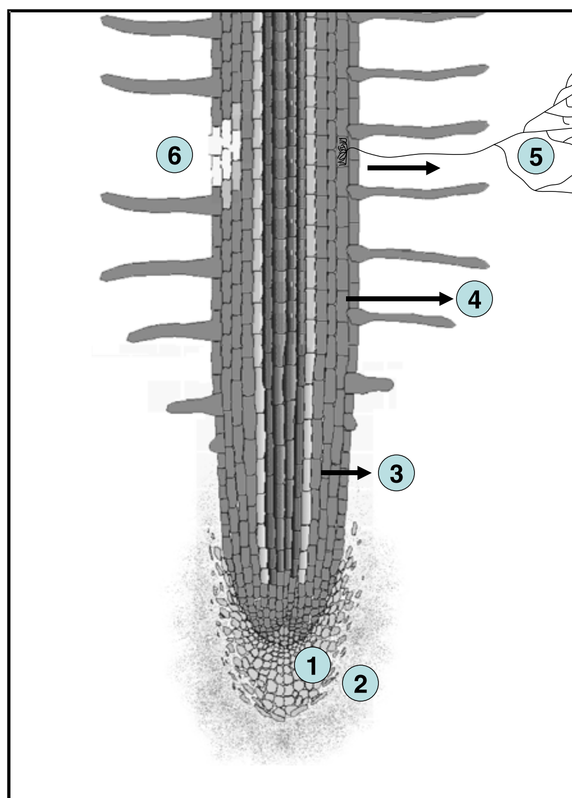


Fig. 1 Schematic representation of a longitudinal section of a growing root showing the six major sites of rhizodeposition: *1* loss of root cap and border cells, *2* loss of insoluble mucilage, *3* loss of soluble root exudates, *4* loss of volatile organic C, *5* loss of C to symbionts (e.g. arbuscular mycorrhizas), and *6* loss of C due to death and lysis of root epidermal and cortical cells

rapidly in the absence of shoots in a hormone free medium making them suitable for the controlled excretion and collection of secondary metabolites (Srivastava and Srivastava 2007). In our efforts to create a more sustainable environment, it is also clear that rates of release of C compounds from roots can be manipulated to increase food production, enhance water conservation, speed up the remediation of contaminated sites, and reduce the need for artificial fertilizers and pesticides (Lasat 2002; Vessey 2003; Welbaum et al. 2007). Thus while the intricate complexity of the rhizosphere continues to amaze us and presents a real challenge to scientists trying to unravel its diverse web of interactions, it also has the potential to offer great benefits to society. As C flow from roots is essentially the starting point from which the rhizosphere develops it is important that we improve our understanding of this process.

This review aims to critically assess our current understanding of rhizosphere C flow and to highlight areas for further research. Due to the large number of publications in this research area (>5000 individual publications) it is not our aim to cover the entire literature but to highlight examples to support themes. Readers requiring more comprehensive historical reviews of the literature should consult Rovira (1969), Curl and Truelove (1986), Lynch (1990) and Pinton et al. (2001).

Roots release a great variety of compounds by different mechanisms

Virtually, all compounds contained in root tissues can be released into the soil. In hydroponic culture, carbohydrates, organic and amino acids, phenolics, fatty acids, sterols, enzymes, vitamins, hormones, nucleosides have been found in the root bathing solution (Rovira 1969; Grayston et al. 1996; Dakora and Phillips 2002; Read et al. 2003; Leinweber et al. 2008). These compounds are released by various mechanisms including secretion, diffusion or cell lysis. Depending upon the question being addressed, different nomenclatures for rhizodeposits have been proposed based for instance on the mechanisms of release, on the biochemical nature of rhizodeposits or on their functions in the rhizosphere. The classification first proposed by Rovira et al. (1979) is generic and has been extensively used.

Mucilage

Root mucilage forms a gelatinous layer surrounding the root tip and is one of the few clearly visible signs of organic C excretion from roots (Fig. 2). It is mainly composed of polysaccharides of 10^6–10^8 Da in size (Paull et al. 1975) and is actively secreted by exocytosis from root cap cells (Morre et al. 1967; Paull and Jones 1975a, b, 1976a, b). Alongside polysaccharides, it also contains proteins (ca. 6% of dry weight; Bacic et al. 1987) and some phospholipids (Read et al. 2003). In most situations mucilage released into the soil confers a wide range of benefits to the plant. For example, the carboxylic groups of mucilage can complex potentially toxic metals (e.g. Al, Cd, Zn, Cu), protecting the root meristem (Morel et al. 1986; Mench et al. 1987). In addition, mucilage enhances soil aggregate stability which in the long-term promotes soil aeration, root growth and reduces

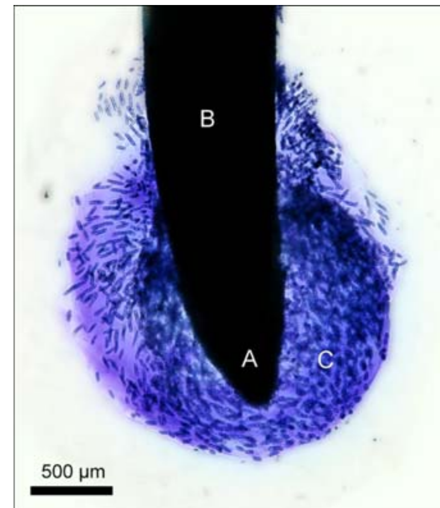


Fig. 2 Light microscope image showing the large amount of mucilage (*blue* halo surrounding the root) and border cells production in a *Zea mays* L. root tip. *Labels* indicate the root quiescent centre (*A*), the main root elongation zone (*B*), and the mucilage halo in which the border cell are embedded (*C*). The mucilage is stained with *aniline blue*

soil erosion (Guckert et al. 1975; Morel et al. 1990; Czarnes et al. 2000). Mucilage also possesses a high intrinsic affinity for water and when fully hydrated, has a water content 100,000 times greater than its dry weight (McCully and Boyer 1997) and expands to form a viscous droplet covering the root tip. Such properties play a role in maintaining the continuity of water flow towards the rhizoplane (Read and Gregory 1997; Read et al. 2003) and in reducing the frictional resistance as the root tip moves through the soil (Iijima et al. 2004). Recent work has also suggested that specific mucilage components (e.g. prenylated stilbenes) possess antimicrobial properties and may be important in preventing pathogen attack (Sobolev et al. 2006). Apart from the C employed to synthesize and secrete mucilage, its loss into the soil appears to have no known negative effects on soil and plant health. Of most concern is that mucilage represents a source of labile C in the soil and is consequently rapidly consumed by soil microorganisms (typical half-life of 3 days). In some instances this can induce the proliferation of root rot disease-causing organisms in the rhizosphere (e.g. *Pythium aphanidermatum*; Zheng et al. 2000) while in other situations due to its high C:N ratio (ca. 65), its biodegradation induces a transient net immobilisation of N in the rhizosphere (Mary et al. 1993; Nguyen et al. 2008). While

increasing the rate of polysaccharide mucilage release from roots is possible and would only constitute a minor C drain (Darrah 1991a), it is unlikely to yield major benefits in comparison to alteration in other rhizodeposition processes.

Border cells

Also called sloughed-off cells, border cells are the cells that detach from the external layers of the root cap, which is continuously renewed (Barlow 1975; Fig. 2). The controlled separation of the border cells reduces the frictional force experienced by the root tip (Bengough and McKenzie 1997; Bengough and Kirby 1999; Iijima et al. 2004). The daily rate of border cell production is highly variable among plant species, from none to tens of thousands with release rates highly dependent upon the prevailing environmental conditions (Hawes et al. 1998; Iijima et al. 2000; Zhao et al. 2000). Once detached from the cap, border cells remain alive in the soil for several days (Stubbs et al. 2004). They are surrounded by the mucilage they secrete, which binds heavy metals away from the root meristem (Miyasaka and Hawes 2001). Border cells also produce signal compounds involved in the protection of meristem against pathogens (Hawes et al. 2000) and in the promotion of symbiosis (Brigham et al. 1995; Hawes et al. 1998). Recent work has also suggested that border cells can act as a decoy luring pathogenic nematodes and fungi away from the main root axis (Gunawardena and Hawes 2002; Rodger et al. 2003). However, contradictory results have also been found highlighting the difficulties of manipulating border cell release and physiology for disease control (Wuyts et al. 2006; Knox et al. 2007). While border cells may provide a convenient mechanism for compound delivery to soil, further fundamental work is required to characterise the metabolomic and proteomic expression patterns in comparison to other root cells to understand and capitalize on their unique attributes (Jiang et al. 2006). In the total rhizodeposition C budget, however, border cells only constitute a small proportion of the C entering the soil (Iijima et al. 2000; Farrar et al. 2003).

Exudates

Exudates are defined as diffusible compounds which are lost passively by the root and over which the root exerts little direct control. Rates of loss of individual compounds depend upon three critical factors, namely (1) the root-soil concentration gradient, (2) the permeability of the plasma membrane, and (3) the spatial location of the solutes in the root tissue (e.g. epidermis versus stele). The dominant organic compounds in roots reflect those compounds central to cell metabolism and include free sugars (e.g. glucose, sucrose), amino acids (e.g. glycine, glutamate) and organic acids (e.g. citrate, malate, oxalate; Kraffczyk et al. 1984). Their concentration inside the root is typically orders of magnitude greater than that in the surrounding soil solution due to continual removal from the soil by the soil microbial community and replenishment of internal pools by the root. Although we know a great deal about the concentrations of solutes in whole roots our understanding of the spatial and temporal dynamics of organic solutes in roots is severely limited. As there is significant internal partitioning of solutes in root cells (e.g. cytoplasm versus vacuole; Gout et al. 1993; Ciereszko et al. 1999), of critical importance is the actual concentration gradient that exists between the cytoplasm and the cell wall space rather than that between the whole root and bulk soil. In addition, at a tissue level, the role of the cortex in root exudation versus that of the epidermis remains unknown. Although apoplastic loss may represent a slow diffusion pathway in comparison to direct loss from the epidermis (Canny 1995; Fleischer and Ehwald 1995), evidence suggests that gaps between epidermal cells (where apoplastic loss ultimately manifests itself) are strong regions of microbial colonization and therefore C availability (Quadt-Hallmann et al. 1997; Watt et al. 2006). Therefore more work is required to characterise apoplastic loss pathways from the root cortex and its contribution to maintaining the endo- and ecto-rhizosphere microbial community. Further work is also required to determine the temporal dynamics of solutes in root tissues (e.g. diurnal versus ontogenetic) and the relationship with exudation.

The cytoplasmic pH of most root cells ranges from 7.2–7.5. Within this range most organic acids are negatively charged while most amino acids and sugars carry no net charge. Due to plasma membrane H^+-ATPases pumping H^+ out of the cells, the outside of the plasma membrane carries more positive charge than the inside (Fig. 3). Consequently, there is a greater tendency for anionic organic solutes to be

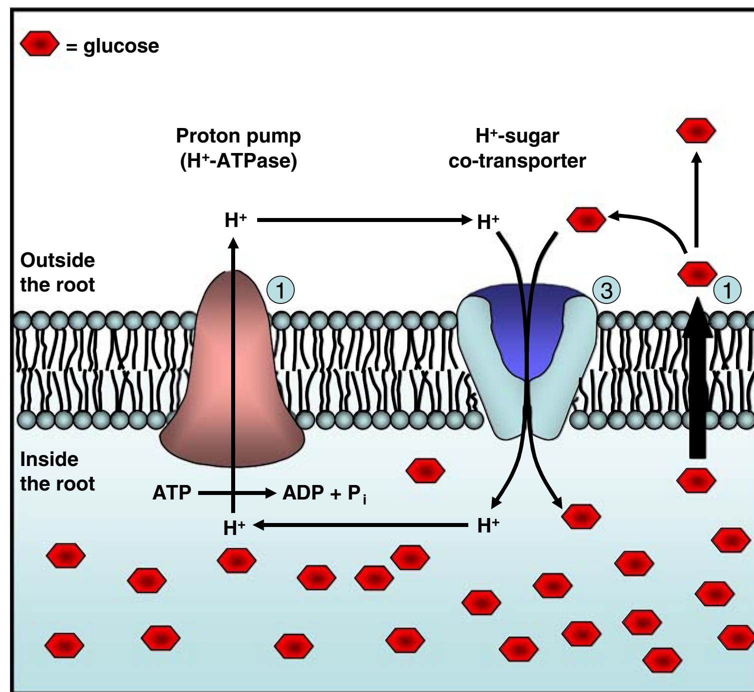


Fig. 3 Schematic representation of the three main processes involved in the bi-directional flux of low molecular weight organic solutes (e.g. glucose) across the soil root interface. Flux (*1*) denotes the passive transport of glucose across the plasma membrane in response to the large cytoplasm (20 mM) to soil solution (10 μM) concentration gradient. Flux (*2*) denotes the active energization of the plasma membrane by the H^+-ATPase which pumps H^+ out of the cell using ATP as the energy source. Flux (*3*) denotes the active re-uptake of sugars from the soil solution back into the cytoplasm using a H^+-cotransport protein. The cell wall is not drawn for clarity

drawn across the membrane at faster rates than non-charged solutes (Ryan et al. 2001). Studies in non-plant systems suggest that although solutes can diffuse through the lipid bilayer, faster rates of diffusion occur at the lipid–protein boundary. Further, organic solute loss may be accelerated at sites where active growth is occurring as membrane vesicle contents are released during fusion with the plasma membrane. Rates of exudation can also be greatly speeded up by the opening of solute specific channels in the membrane. Probably the best known example of this is the release of organic acids when roots experience either P deficiency or high external concentrations of free toxic Al^{3+} (Zhang et al. 2004; Ligaba et al. 2006). The release of organic acids such as citrate, malate and oxalate can complex the Al^{3+} rendering it non-toxic. Detailed reviews of the role of organic acid channels in metal detoxification and nutrient uptake (e.g. P) can be found in Ryan et al. (2001), Jones et al. (2004) and Roberts (2006).

Generally, rates of exudate loss are greater at root tips in comparison to mature root regions (McDougal and Rovira 1970; Hoffland et al. 1989). Potential reasons to explain this enhanced C loss from tips include: (1) higher solute concentrations in root tip regions thereby creating a larger diffusion gradient (Jones and Darrah 1996; Jones et al. 1996), (2) small vacuolar volume of root tip cells inducing higher cytoplasmic concentrations (Patel et al. 1990), greater surface area-to volume ratio of tip cells, (3) the lack of an endodermal layer to minimize cortical loss (Schraut et al. 2004), (4) increased rates of apoplastic solute unloading from the vascular tissue leading to greater apoplastic loss (Bockenhoff et al. 1996), (5) greater apoplastic volume inducing higher rates of solute diffusion (Kramer et al. 2007), (6) higher rates of growth in tip regions and therefore solute loss during vesicle fusion and signalling events (Beemster and Baskin 1998; Roux and Steinebrunner 2007), and (7) localized loss of root border and cap cells which may undergo apoptosis releasing solutes (Shishkova and Dubrovsky 2005). Like many other aspects of rhizodeposition our conceptual understanding is good, however, our detailed mechanistic understanding of

the relative importance of the individual flux pathways remains poor and this must remain as a priority for future research.

Secretions (excluding mucilage)

Plant roots actively secrete various compounds in response to a range of environmental conditions and our understanding of the role of these compounds in rhizosphere processes often remains poor (Wen et al. 2007). One exception is the characterisation of phytosiderophore release by grasses under conditions of low Fe availability (Negishi et al. 2002). In this situation, Fe-phytosiderophore complexes are also actively taken back into the plant (Haydon and Cobbett 2007). Phenolics are also secreted from roots and have been implicated in the mobilization of nutrients such as Fe and P, however, their quantitative importance remains unknown (Dakora and Phillips 2002). Enzymes (e.g. phosphatase) and many other compounds such as secondary metabolites may also be secreted into the rhizosphere and participate in the interactions between the roots and their environment (Bais et al. 2004). High molecular weight compounds or toxic molecules are likely to be released by exocytosis (Verpoorte et al. 2000). However, the mode of release is not always clearly established and much further work is required to elucidate mechanisms of release and their quantitative significance in the soil.

Senescence-derived compounds

Depending upon the conditions experienced by the root, a variable part of the epidermis including root hairs and of the cortical cells can degenerate and release their content into the rhizosphere (Fusseder 1987; McCully 1999). As roots rarely senesce in hydroponic culture, this process is largely thought to occur in soil where pathogens and mineral abrasion can induce cell death. Little is known about the magnitude of this flux pathway as it is almost impossible to study in soil. Consequently, most measurements typically rely on quantifying the amount of epidermal and cortical cell loss rather than the amount of C transferred to the soil. The amount entering the soil can be expected to depend upon whether the roots undergo programmed (apoptosis) or spontaneous cell death, however, little is known about the relative importance of these two processes. However, we do know that plant roots contain a significant amount of soluble and insoluble C and that their death will results in a significant C and N input to the soil and an elevation of microbial populations in their necrosphere (McClaugherty et al. 1982; Nadelhoffer and Raich 1992; Stewart and Frank 2008). Typically, there is a positive correlation between root diameter and lifespan (Gill and Jackson 2000). Consequently, in temperate agricultural grasslands containing an abundance of fine roots, we can calculate the magnitude of the C input to soil from root turnover. The soil organic C content of a temperate, grazed grassland soil typically ranges from 10 to 50 g C kg soil^{-1} while the standing root biomass typically ranges from 5 to 15 g root-C kg soil^{-1} and the microbial biomass from 0.5 to 1 g C kg soil^{-1} of which we assume only 10% is active (Jones, unpublished). It has been estimated that in the growing season approximately 25% of the roots turn over each month equating to approximately 2 to 10 g C kg soil^{-1} month^{-1} (i.e. enough C to generate 50 to 100 times the size of the active microbial biomass in soil). This can be compared to the rates of C exudation from grass roots which typically range from 1 to 10 mg C g root-C^{-1} day^{-1} (Hodge et al. 1997; Paterson and Sim 1999; Paterson et al. 2003). Consequently, we can estimate the amount of C entering grassland soils from root exudation to be in the range 0.1 to 5 g C kg soil^{-1} month^{-1} similar to that derived from root turnover.

Carbon flow to mycorrhizal and bacterial symbionts

Apart from the bacterial-legume symbiosis which has been reviewed extensively, little is known about the flow of C to other bacterial symbionts in the rhizosphere (Dilworth et al. 2008; Ohyama et al. 2009). Consequently, here we will focus on mycorrhizas. Most plants in natural and semi-natural vegetation systems form symbiotic associations with mycorrhizal fungi and there is increasing evidence to suggest that the flow of C to and through this symbiotic interface may be of significance in many plant–soil interactions, playing an important role in different biogeochemical processes (Finlay and Rosling 2006; Finlay 2008). Mycorrhizal symbionts contribute to carbon flow in the rhizosphere in three main ways. Firstly, the investment of C in production of

biomass of intra- and extraradical mycelial structures is, in itself, substantial (Leake et al. 2004). Secondly, there is a flow of C through these structures, resulting in release of a range of exudates into the mycorrhizosphere, and thirdly, these compounds, and the mycorrhizal mycelium itself, can be used as energy rich substrates by other organisms, resulting in respiratory loss of carbon as CO_2. As with studies of other components of rhizodeposition, considerable effort has been directed at quantifying the contribution of these processes in relation to total rhizosphere C flow, whilst fewer studies have focused on their potential functional roles.

Because of their fine dimensions and fragility, mycorrhizal hyphae are even more difficult to study than fine roots. The mycelium is easily damaged when excavating roots, it consists of viable and non-viable fractions and must be distinguished from the mycelia of saprotrophic and pathogenic fungi. Despite these difficulties, much knowledge has been gained about the structure, biology and impact of mycorrhizal mycelia (see Leake et al. 2004 for an extensive review). Over 50 estimates of mycelial production by arbuscular mycorrhizal (AM) fungi or ectomycorrhizal (EM) fungi are cited from a range of pot and field studies. Estimates of hyphal length for AM fungi typically range from 3–30 m g^{-1} soil but 68–101 m g^{-1} soil have been recorded in undisturbed grasslands with permanent plant cover. EM hyphae are more difficult to distinguish morphologically from saprotrophic fungi and hyphal length estimates are less reliable but available data suggest hyphal length densities of between 3 to 600 m g^{-1} soil. Wallander et al. (2001) used a combination of techniques such as in-growth mesh bags, measurements of fungal markers such as phospholipid fatty acids and ergosterol, $\delta^{13}C$ values and trenching to distinguish mycorrhizal fungi from soil dwelling saprotrophs. The total amount of EM mycelium colonising the mesh bags was calculated to be 125–200 kg ha^{-1} and the total amount of EM mycelium, including EM mantles was estimated to be 700–900 kg ha^{-1}.

Clearly the investment of C in mycelial structures is considerable and many attempts have been made to estimate C allocation to mycorrhizal mycelium. Many of these involve labelling studies with radioactive or stable isotopes and are subject to different sources of error. Microcosm studies may result in unnaturally high mycelial biomass and/or exclude soil biota which may graze fungal mycelia. However, short pulse-labelling experiments may underestimate C allocation to mycorrhizal mycelia since they only measure cytoplasmic allocation and exclude C allocation to previously formed fungal cell walls. Many experiments fail to measure respiratory losses of labelled CO_2 which complicates the construction of complete C budgets. C flow through arbuscular mycorrhizal (AM) mycelia has been measured in grassland ecosystems dominated by AM mycelia and found to be at least as large as that of fine roots, with at least 5.4–7.7% of the C lost by plants being respired from AM fungal mycelium and 3.9–6.2% being fixed in mycorrhizal mycelium within 21 h of labelling (Johnson et al. 2002). These figures are comparable with those for fine roots and suggest that there is a very rapid flux of C through mycorrhizal hyphae. A particular strength of these data is that they were obtained under field conditions. Additional studies using similar methods have investigated the effects of soil invertebrates and shown that they can disrupt C transport through hyphal networks but that there is still a significant, rapid flow (Johnson et al. 2005). Analyses of ^{14}C content of AM hyphae by accelerator mass spectrometry (Staddon et al. 2003) suggest that most hyphae live for 5–6 days, again suggesting that there is a large and rapid pathway of C flow through the AM extraradical mycelium.

Measurements of C flow to ectomycorrhizal mycelium colonising forest trees are more difficult to obtain due to the size of the plant hosts, but data from smaller plants in microcosm systems (Leake et al. 2001) showed that the extraradical mycelium of the ectomycorrhizal fungus *Suillus bovinus* colonising *Pinus sylvestris* seedlings contained 9% of the ^{14}C contained in the plants 56 h after labelling. Over 60% of the C allocated to the extraradical mycelium was allocated to mycelium colonising patches of litter, which only represented 12% of the available area for colonisation, suggesting that this C allocation was associated with nutrient acquisition. Data from a range of microcosm-based labelling studies (see Leake et al. 2004 for details) suggest that 7–30% of net C fixation is allocated to ectomycorrhizal mycelium and that 16–71% of this C is lost as respiration. These data are likely to be underestimates of C transfer to the mycelium since short term pulse-labelling experiments do not measure the carbon in the fungal cell walls. Although microcosm experi-

ments may not accurately reflect field conditions, manipulation of the ectomycorrhizal extraradical mycelium in forest ecosystems using the methods employed by Johnson et al. (2002) is not possible due to the large size of the plants. Tree girdling experiments in a 45–55 year old pine forest by Högberg et al. (2001), however, suggest that soil respiration is directly coupled to the flux of current assimilate to mycorrhizal roots and fungi. Decreases of 37% were recorded within 1–2 days, however, this method does not allow separate determination of the root and fungal components. Further observations following a large-scale girdling experiment suggest that ectomycorrhizas may contribute at least 32% of soil microbial biomass and as much as half the dissolved organic carbon in forest soil (Högberg and Högberg 2002). The below-ground flux of recent photosynthate has been followed with high temporal resolution using ^{13}C labelling of 4-m-tall *Pinus sylvestris* trees (Högberg et al. 2008). C in the active pools in needles, soluble carbohydrates in phloem and in soil respiratory efflux had half-lives of 22, 17 and 35 h, respectively. C in soil microbial cytoplasm had a half-life of 280 h, while the C in ectomycorrhizal root tips turned over much more slowly. Simultaneous labelling of the soil with $^{15}NH_4^+$ showed that the ectomycorrhizal roots, which were the strongest sinks for photosynthate, were also the largest sinks for N. Tracer levels peaked after 24 h in the phloem, after 2–4 days in the soil respiratory efflux and soil microbial cytoplasm and 4–7 days in the ectomycorrhizal roots. The results indicate close temporal coupling between tree canopy photosynthate and soil biological activity. Other recent studies using free air carbon dioxide enrichment (FACE) experiments as a means of ^{13}C labelling (Körner et al. 2005) and bomb ^{14}C estimates of root age (Gaudinski et al. 2001) suggest that fine roots of trees may turn over much more slowly than previously assumed. This suggests that more of the below-ground C flux may take place through mycorrhizal fungi and other soil biota associated with roots (Högberg and Read 2006). A recent FACE study of a *Populus* plantation supports this idea, suggesting that extraradical mycorrhizal mycelium is the dominant pathway (62%) through which C enters the soil organic matter pool (Godbold et al. 2006).

Both arbuscular mycorrhizal and ectomycorrhizal plants can regulate their C allocation to roots. *Trifolium repens* plants have been shown to increase their rates of photosynthesis in response to increased sink strength of mycorrhizal roots and to increase activities of cell wall and cytoplasmic invertases and sucrose synthase (Wright et al. 1998). In ectomycorrhizal plants the symbiotic partners receive up to 19 times more carbohydrates from their roots than normal leakage would cause, resulting in a strong C sink. To avoid parasitism the plants appear to have developed mechanisms to regulate the C drain to the fungal symbiont in relation to the supply of fungus-derived supply of nutrients (Nehls 2008). Increased expression of plant and fungal hexose transporter genes has been detected at the plant fungus interface in ectomycorrhizas, but it appears there may also be mechanisms to restrict carbohydrate loss to the fungus. Hexoses generated from sucrose hydrolysis by plant-derived acid invertases could be taken up by plant or fungal cells through monosaccharide transporters. One Poplar sugar transporter gene (*PttMST3.1*) is expressed at least 10 times more highly than other hexose transporter genes and it is postulated that this may be regulated at the post-transcriptional level by phosphorylation which would allow activation of the transporter as a reaction to the amount of nutrients delivered by the fungus. If the fungus provided sufficient nutrients the activity of the transporter would be shut off, while the protein would be activated as soon as the nutrient transfer is insufficient (Nehls 2008). Unpublished data support this hypothesis but further studies of the genetic basis of regulation of carbon flow at the symbiotic interface are still needed in a range of different mycorrhizal associations.

One disadvantage of simple labelling experiments showing transport of a labelled element from a source to a sink is that they provide no information about *net* movement of the element in question, since there may be an equal (or greater) movement of the same (unlabelled) element in the reverse direction. The issue of C transport between plants connected by a common mycorrhizal mycelium has been controversial. Experiments by Francis and Read (1984) demonstrated the potential for transfer of C along concentration gradients from sources to sinks induced by shading, however, these studies were criticised for the above reasons. Experiments by Simard et al. (1997) using reciprocal labelling with ^{14}C and ^{13}C demonstrated net transfer of C from *Betula papyrifera* to *Pseudotsuga menziesii* but the overall ecological

significance of inter-plant C transfer has been questioned by Robinson and Fitter (1999). NMR studies of common AM mycelial networks by Pfeffer et al. (2004) revealed that, although significant amounts of C were transferred between different roots connected by a common fungal mycelium, the labelled C remained within fungal compounds and no transfer of C from fungus to plant took place. As pointed out by Pfeffer et al. (2004) and earlier by Finlay and Söderström (1992) such distribution of C within mycelial networks may be of significance even in the absence of net transfer of C from fungus to plants since it would reduce the C demand of the fungal mycelium colonising newly connected host plants and enable them to gain access to nutrients taken up by the mycelium. Although the predominant movement of C in fully autotrophic mycorrhizal hosts is likely to be from plant to fungus, over 400 plant species are achlorophyllous and described as '*myco-heterotrophic*', obtaining their C from fungi. DNA-based studies of these fungi have revealed most of them to be mycorrhizal species colonising other autotrophic plants. The mycoheterotrophic species are thus effectively 'cheaters' or epiparasites obtaining their C and nutrients through mycorrhizal connections with neighbouring autotrophic plants (Bidartondo 2005; Bidartondo et al. 2002; Leake 2004). In orchids the direction of C transfer is often reversed since about 100 species are completely achlorophyllous and all others pass through a germination and early developmental phase in which they are dependent on an external supply of nutrients and C since they have minute, dust-like seeds with no reserves. Survival of germinating seedlings is thus dependent upon rapid integration into fungal mycelial networks. Although this pathway of C transfer is sometimes dismissed as a 'special case' in discussions concerning the overall significance of C transfer via mycorrhizal hyphal connections, the Orchidaceae is the largest family in the plant kingdom with over 30,000 species so the habit is arguably widespread and of evolutionary significance.

Acquisition of N (Bending and Read 1995) and P (Lindahl et al. 2001) by ectomycorrhizal fungi colonising organic substrates is dependent on resources allocated to the mycelium. Ectomycorrhizal and ericoid mycorrhizal fungi play a pivotal role in the mobilisation of N and P from organic polymers (Read and Perez-Moreno 2003) and their enzymatic capacities have been reviewed by Lindahl et al. (2005). Increased ectomycorrhizal mycelial growth and biomass production, resulting in selective spatial allocation of C to nutrient rich substrates has been demonstrated in a range of studies (see Read and Perez-Moreno 2003) and been shown to be associated with mobilisation of N and P. Energy is undoubtedly required for the synthesis of enzymes involved in the mobilisation of nutrients but the partitioning of C between fungal biomass production and hydrolytic activity is not yet fully understood. Experiments by Lindahl et al. (2007) suggest that decomposition of litter by saprotrophs and mobilisation of N from well-decomposed organic matter may be spatially and temporally separated in boreal forests. Many of the organic N compounds taken up by ectomycorrhizal mycelium contain C derived from photosynthetic products originally translocated to the soil via the same mycelium. This may reduce the C drain imposed upon the host plant by ectomycorrhizal symbionts. In axenically grown *Betula pendula* plants supplied with ^{14}C labelled protein as the sole exogenous N source, only ectomycorrhizal plants were able to exploit this N source. Heterotrophic uptake of C associated with utilisation of this organic N source was estimated to be up to 9% of plant C over a 55 day period (Abuzinadah and Read 1989). Simple amino acid sources are taken up intact by a range of mycorrhizal plants as demonstrated in field experiments by (Näsholm et al. 1998) and this also contributes to the reverse flow of C through the rhizosphere to plant roots. Utilisation of organic N sources by arbuscular mycorrhizal plants is less well understood but Hodge et al. (2001) demonstrated enhanced decomposition and capture of N from decaying grass leaves in the presence of AM fungi. Further experiments are needed to distinguish between direct capture and uptake of organic N by the hyphae and indirect uptake of inorganic N through enhanced decomposition. It is possible that mycorrhizal hyphae contribute to rhizosphere priming via a release of energy rich C which is utilised by microbial saprotrophs. The mycorrhizal mycelium provides a vastly increased surface area (compared with roots alone) for interactions with other microorganisms and an important pathway for translocation into the soil of energy-rich compounds derived from plant assimilates. Soluble C compounds released by the extraradical mycelium of arbuscular fungi have been shown to influence the activity of

both fungi and bacteria associated with the mycorrhizosphere (Filion et al. 1999; Toljander et al. 2007). Both stimulatory and inhibitory interactions are possible and these have been reviewed with respect to their relevance in sustainable agriculture by Johansson et al. (2004). Production of mycorrhizal mycelial exudates has been shown to influence bacterial species composition and vitality (Toljander et al. 2007) and vitality of mycorrhizal hyphae in turn has been shown to influence attachment of different bacteria to AM hyphae (Toljander et al. 2006). Other recent experiments indicate that AM fungi may influence bacterial assemblages in roots but that the effect is not reciprocal (Singh et al. 2008). AM fungi also produce a glycoprotein, glomalin, which is deposited in soil as hyphae senesce and has been estimated to constitute as much as 5% of soil C (see Treseder and Turner 2007). As well as playing a role in soil aggregation glomalin production is thought to sequester significant amounts of C on a global scale (Treseder and Turner 2007).

Exudation and reabsorption of some C compounds from fluid droplets produced at ectomycorrhizal hyphal tips has been demonstrated by Sun et al. (1999) who concluded that it might represent an important mechanism for conditioning the hyphal environment in the vicinity of tips, creating an interface for the exchange of nutrients and C compounds with the adjacent soil environment and its other micro-organisms. Ectomycorrhizal fungi produce significant amounts of organic acids (Sun et al. 1999; Ahonen-Jonnarth et al. 2000) which may play a role in weathering of minerals, complexation of toxic Al^{3+} or in antibiosis. The microbial decomposition of these organic acids could also contribute significantly to soil respiration (van Hees et al. 2005). Experiments by Rosling et al. (2004a, b) suggest that mycorrhizal and other fungi differ in their ability to allocate C to different mineral substrates and that more labelled C is allocated to easily weatherable minerals such as potassium feldspar than to quartz.

Despite the fact that the rhizosphere is defined in terms of its elevated levels of soil microbiological activity, we still know surprisingly little about the role of rhizosphere communities in C flow, and little is known about the roles of different members of the community in assimilating plant exudates. Experiments by Ostle et al. (2003) and Rangel-Castro et al. (2005a) demonstrated rapid allocation and incorporation of recently photosynthesized ^{13}C into soil microbial biomass. Labelled C is incorporated within hours and the half life of microbial pools of ^{13}C was calculated to be 4.7 days. RNA-based stable isotope probing experiments by Rangel-Castro et al. (2005b) using DGGE analysis of bacterial, fungal and archaea, showed that active communities in limed soils were more complex than those in unlimed soils and were more active in utilization of recently exuded ^{13}C compounds. This suggests that in unlimed soils the active microbial community may have been utilizing other sources of C but the results may also reflect differences in the amount of root exudation in limed and unlimed grasslands. Another approach which has been used to study bacterial communities associated with mycorrhizal and non-mycorrhizal root systems is the use of symbiosis-defective plant mutants. In experiments by Offre et al. (2008), Oxalobacteraceae isolates were more abundant in mycorrhizal roots of *Medicago truncatula* than in non-mycorrhizal roots of symbiosis-defective plants, whereas *Comamonadaceae* isolates were more abundant in non-mycorrhizal roots.

New approaches based on stable isotope probing, RNA analysis, and metagenomics (Vandenkoornhuyse et al. 2007) indicate that there are many hitherto unidentified root symbionts and that bacteria and AM fungi occupying roots show differential activity in C consumption with much higher C flow to some fungi than others. Therefore, while it is clear that symbionts are important determinants of rhizodeposition, our understanding remains poor in many respects. While this article is about C flow in the rhizosphere, and there has been a general tendency in rhizosphere research to concentrate on “quantitatively significant” C fluxes, it should be remembered that plants produce a wide spectrum of chemicals which are usually called secondary metabolites because of their presumed secondary role in plant growth. Chemicals released in the rhizosphere play vital roles in signalling between plant roots and different microorganisms. Although these chemicals may only constitute a small proportion of the total photosynthetically derived C flow from roots they can play a key role in plant survival through defence against pathogens or in attracting beneficial symbionts. One example of this is the strigolactones, that are produced in the root exudates of many monocot and dicot species (Bouwmeester et al. 2007). These compounds induce branching of arbus-

cular mycorrhizal fungi but also stimulate the germination of seeds of parasitic plants (*Striga* and *Orobanche* spp.). However, infection by *Striga* is reduced in plants colonised by AM fungi through down-regulating the production of the germination stimulant. Phosphate starvation is known to induce strigolactone production, and also to favour AM colonisation, while AM fungi are known to improve the P status of their hosts, which in turn would repress strigolactone production. The effects of environmental factors on numerous other signalling molecules are still entirely unknown, although their effects on plant growth and survival may be of paramount importance. Therefore, although more quantitative studies of C and N flux in the rhizosphere are still needed, these should also be complemented by further qualitative studies of the role of different signalling molecules, the roles these play in plant–soil–microbe interactions and the way in which they are influenced by different environmental conditions.

Carbon flow in the rhizosphere is bi-directional

Prior to 1990, the general consensus was that rhizodeposition was a unidirectional flux whereby plant C was lost from roots into the soil (Curl and Truelove 1986). Once in the soil it was assumed to undergo a number of fates including movement away from the root in the soil solution due to diffusion and mass flow, capture by soil microorganisms, and sorption to the solid (Martin 1975; Newman and Watson 1977). However, experiments undertaken in hydroponic culture and subsequently soil revealed that plant roots can also take up a range of organic compounds from the soil into the roots with subsequent transfer to the shoots (Jones and Darrah 1992, 1993, 1994). Of the compounds investigated so far, roots from a range of species have been shown to take up predominantly low molecular weight solutes such as organic acids, sugars and amino acids (Jones and Darrah 1995; Sacchi et al. 2000; Thornton 2001). In addition, roots may also take up inorganic C from outside the root when present in a dissolved form (e.g. HCO_3^-; Cram 1974; Amiro and Ewing 1992; Ford et al. 2007). Although HCO_3^- can be readily converted to organic acids inside the root, the contribution of this inwardly directed inorganic C flux to the overall C economy of the plants is small especially in view of the large amount of HCO_3^- generated in respiratory processes (Ford et al. 2007). One potential exception occurs within proteoid roots of lupin roots where significant uptake and assimilation of HCO_3^- into malate and citrate occurs (Johnson et al. 1996). These HCO_3^- derived organic acids are then exuded back into the soil to aid in P mobilization in the rhizosphere.

Discrimination also needs to be made between organic C that is taken up and assimilated in a controlled (i.e. active transport) way and that which is inadvertently taken up as a consequence of its physicochemical properties (i.e. passive transport). In the case of compounds with a high octanol–water partition coefficient (K_{OW}) value, these can simply become sorbed to cell membranes and subsequently metabolised (e.g. pesticides, chlorinated hydrocarbons; Scheunert et al. 1994). This passive process can be expected to have no positive benefit to the plant. Similarly, positively charged organic compounds can become sorbed to cell walls with no subsequent assimilation. Some neutrally charged compounds (e.g. acetic acid) can also passively enter the cell if the concentration outside is greater than that inside. While this has been used as an experimental tool to understand membrane function its significance in soil remains unknown (Herrmann and Felle 1995).

Of greatest ecological significance is the active root uptake of sugars and organic nitrogen compounds (e.g. amino acids, polyamines etc) from soil. Typically, these compounds are taken into the plant by co-transporters which are constitutively expressed and located throughout the root system (Jones and Darrah 1994, 1996; Fig. 3). These co-transporters are powered by the plasma membrane H^+-ATPases which are predominantly located in the epidermis rather than in the root cortex although levels of H^+-ATPases are also high in the stellar regions (Samuels et al. 1992; Jahn et al. 1998). The transport proteins simultaneously transport H^+ across the plasma membrane together with individual organic solutes. The transporters are also relatively solute specific with transport families for amino acids and sugars being well characterised at both the physiological and molecular level (Fischer et al. 1998; Williams et al. 2000; Hirner et al. 2006). In addition, membrane transporters also exist for other solutes such as peptides, flavonoids and polyamines although these protein families remain less well characterised (DiTomaso et al.

1992; Hart et al. 1992; Buer et al. 2007; Jones et al. 2005a, b). There is also strong evidence to suggest that plant roots can take up larger molecular weight solutes by endocytosis (Samaj et al. 2005). Current evidence suggest that this process is important for auxin-mediated cell–cell communication, polar growth, gravitropic responses, cytokinesis and cell wall morphogenesis (Ovecka et al. 2005).

As the plant expends energy in the uptake of these compounds from soil we assume that the process must confer some benefit to the plant. At present there are four principal hypotheses to explain why plants might take up organic solutes from soil (Fig. 4). Although there is no reason to suggest that these are mutually exclusive it is likely that their importance varies in space and time within a root system and between plant species.

Hypothesis 1: direct root exudate recapture

The first explanation is that the root is simply recapturing C back from the soil that it previously lost in response to passive root exudation, the latter being a process over which it exerts little direct control (Jones et al. 1996). This recapture of exudate C not only enhances C use efficiency in the plant but also prevents C accumulation in the rhizosphere thereby reducing the growth of the soil microbial community. This may serve three purposes by (1) reducing microbial competition for poorly available nutrients required by the root (e.g. N and P), (2) reducing the growth of potentially pathogenic organisms, and (3) minimizing chemotactic gradients for pathogenic organisms. When chemotaxis of beneficial organisms is required, current evidence suggests that more chemically specific signals at low concentrations are released in root exudates in a spatially and temporally controlled manner (e.g. flavonoids; Antunes et al. 2006; Sugiyama et al. 2007).

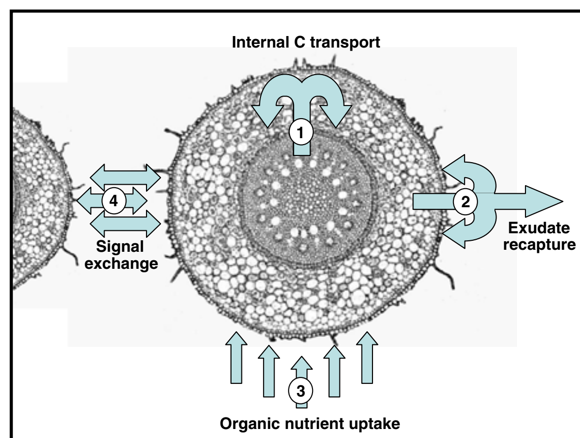


Fig. 4 Schematic representation of a transverse root section illustrating the four principal hypotheses explaining the uptake of organic C from soil: *1* indirect, fortuitous root exudate recapture in the root's internal apoplastic transport and signalling pathways, *2* direct recapture of root exudates from the soil with the aim of reducing microbial growth and pathogen chemotaxis, *3* uptake of organic nutrients (e.g. amino acids) released during the mineralization of soil organic matter in the rhizosphere, and *4* transfer of chemical signals involved in inter-root and root–microbial communication pathways

Hypothesis 2: indirect, fortuitous root exudate recapture

The second explanation is that re-uptake of C from soil might simply be indirectly related to normal source-sink C delivery mechanisms in plants. In most roots, solutes arriving from the shoots are unloaded symplastically from the phloem, however, some subsequently leak into the apoplast where retrieval by active transporters can occur (Eleftheriou and Lazarou 1997; Patrick 1997). This is unlikely to be of significance in areas with a well developed exodermis and tissues with high symplastic connectivity, however, it may be important in root caps and cells where plasmodesmata have been blocked (Zhu and Rost 2000; Hukin et al. 2002). These re-uptake processes may also be indirectly linked to cell wall bound invertases (Huang et al. 2007). These enzymes convert apoplastic sucrose to glucose and fructose which are then taken into the cell by co-localized sugar transporters (Dimou et al. 2005). Import of extracellular hexose sugars has been linked to a range of sensing and signalling pathways in addition to their potential role in supplying sugars for cellular expansion (Sherson et al. 2003).

Hypothesis 3: nutrient capture from soil

The third explanation is that the uptake of organic compounds from the soil may be a mechanism to supply organic nutrients in addition to traditional inorganic uptake routes (i.e. NO_3^-, NH_4^+, $H_2PO_4^-$ etc). This may be particularly relevant in situations where the supply of inorganic nutrients is limiting due to either their low intrinsic solubility (e.g. P), low rate

of ecosystem addition or a block in organic matter mineralization preventing their release back into the soil (e.g. N). It may also be particularly relevant to non-mycorrhizal plants which lack the capability to directly mineralize organic matter. Addition of isotopically labeled organic compounds to soil (^{15}N, ^{13}C, ^{14}C) has shown that roots have the potential to take up and assimilate a wide range of compounds. In agricultural soils, however, it has been shown that plants are poor competitors for amino acids and sugars in comparison to the soil microbial community (Owen and Jones 2001; Bardgett et al. 2003; Kuzyakov and Jones 2006). Consequently, unless concentrations of organic solutes in the soil are very high the uptake of exogenous organic N is likely to be of minimal significance (Jones et al. 2005a, b). In contrast, work in predominantly arctic and alpine soils has suggested that organic N taken up from the soil in the form of amino acids may contribute significantly to a plant's N budget (Chapin et al. 1993). In this case the direct uptake of organic N circumnavigates the need for the soil microbial community to mineralize soil organic matter (Lipson and Nasholm 2001). The uptake of organic N by roots is often viewed in the literature as being unidirectional. The lack of consideration for an outward flux (i.e. root exudation) therefore brings into question many of the rates of flux reported in the literature. In most experiments, rates of organic N uptake into roots are measured with dual ^{15}N-^{13}C labeled compounds. As exudation of organic N is derived predominantly from non-isotopically labeled organic N, due to the large internal organic N reservoir relative to the amount added, most isotopic tracer experiments will greatly overestimate the rates of uptake. What we really require are not measurements of gross rates of uptake, but moreover net rates of uptake (i.e. influx minus efflux; Philips et al. 2006). In the case of amino acids and sugars, measurements in sterile hydroponic culture have shown that the point of net zero uptake (i.e. influx = efflux) occurs when the external concentration is between 0.5 and 10 μM (Jones and Darrah 1994, 1996; Phillips et al. 2004). In most situations this is extremely similar to the concentrations which exist naturally in soil solution (Andersson and Berggren 2005; Jones et al. 2005a, b; Boddy et al. 2007) suggesting that the contribution of organic N uptake from soil may be less important than as a mechanism for retaining the resources it already has (i.e. recapture of exudates). The interpretation of isotopic flux measurements is also complicated by the knowledge that some organic N compounds can be firstly broken down in the soil and the ^{15}N released taken up as $^{15}NH_4^+$ or $^{15}NO_3^-$. Measurements of the relative enrichment of ^{15}N and ^{13}C in the roots can potentially be used to discriminate between ^{15}N taken up in an intact form versus that previously mineralized in the soil. However, after amino acids enter the root they can undergo a number of metabolic reactions that can ultimately lead to approximately 40–60% of the ^{13}C being released as $^{13}CO_2$ (e.g. transamination and deamination; Owen and Jones 2001). Similarly, the loss of organic N derived CO_2 can also occur after uptake by mycorrhizas again leading to an underestimation of the organic N flux. Consequently, isotopic flux measurements are fraught with potential pitfalls that make interpretation of organic C and N fluxes at the root–soil interface extremely difficult (Jones et al. 2005a, b).

Hypothesis 4: rhizosphere signalling

The fourth explanation for plants actively taking up organic compounds from soil is for inter and intra-root signalling and for root–microbial signal exchange. In comparison to the other three potential explanations, this is a poorly explored aspect of rhizosphere ecology (Bais et al. 2004). Although sugars are important in plant signalling, there is currently no evidence to suggest that they would provide specific signals to enable effective communication between roots and other organisms in the rhizosphere. More likely is that root transporters would be involved in the uptake of highly specific signalling molecules (e.g. peptides). In other cases, compounds released from microorganisms can have a direct effect on plant growth and metabolism (Brown 1972), however, the mode of transport of these signalling molecules into the root remains unknown (e.g. lumichrome; Phillips et al. 2004; Matiru and Dakora 2005). As our understanding of the diversity and control of signalling processes in plants increases it is likely that some of these will have functional significance in the rhizosphere (Bais et al. 2004; Bahyrycz and Konopinska 2007; Jun et al. 2008). Further discussion of this issue can be found in Hartmann et al. (2009), Lambers et al. (2009) and Faure et al. (2009).

Rhizodeposition in the plant C and N budget

Methods of investigation

While rhizodeposition can be quantified relatively easily in the absence of soil by growing roots in sterile hydroponic culture and collecting the C accumulating in the external media, this method lacks ecological relevance (Ryan et al. 2001). Quantifying rhizosphere C-flow in relation to soil environments, however, has proved extremely difficult. The amount of rhizodeposition entering soil during a growing season typically represents only a small amount of C and N in comparison to that already present in the soil organic matter (SOM) and therefore measuring changes in soil C in response to rhizodeposition remains virtually impossible. This is also highly pertinent to the uncertainties surrounding the effects of environmental change on the soil C-balance where, although significant effects on soil C-sequestration are predicted, changes in soil C are difficult to detect due to the large SOM-C background and high degree of spatial variability in SOM. Consequently, tracing root-derived C and N by isotopic techniques is a prerequisite for the quantification of rhizodeposition in soil (Warembourg and Kummerow 1991). For C, a widely used technique involves the exposure of shoots to a ^{13}C or ^{14}C enriched atmosphere to label the photoassimilates. Subsequently, the fixed isotope tracer becomes partitioned to range of operationally defined below-ground compartments (roots, soil residues including microbial biomass, and root-derived CO_2). Changes in isotope abundance in these pools is typically followed over time to estimate rhizodeposition as part of the plant or ecosystem C budget. The experimental conditions have to be carefully considered when interpreting the partitioning of photoassimilates. For example, the length of the isotopic labeling and subsequent chase period is a major determinant of the amount of C delivered into the soil (Meharg 1994). Short-term pulse labeling (minutes to hours) traces rhizodeposits derived predominantly from recent photoassimilates (i.e. root exudates, mucilage and border cells). Accordingly, pulse-labeling by this method tends to underestimate total rhizodeposition but remains useful in the investigation of assimilate partitioning in relation to plant metabolism (Phillips and Fahey 2005; Allard et al. 2006; Hill et al. 2007). Longer isotopic labeling periods (weeks to months) trace not only the senescence and turnover of roots but also the fraction of root exudates that may not be derived from recent C (Swinnen et al. 1995). In some cases this may be a significant part of total root exudation (Thornton et al. 2004).

Most experiments in soil have tended to focus on the total amount of C lost in rhizodeposition, while hydroponic studies carried out in the laboratory have tended to focus on the tracking of individual compounds lost from roots. The isotopic tracking of individual root-derived compounds into soil, however, has only recently become routinely possible (Paterson et al. 2008). The use of gas chromatography coupled to isotope ratio mass spectrometry allows the dynamic tracking of specific rhizodeposits such as sugars from roots and associated symbionts into soil (Derrien et al. 2004; Paterson et al. 2007). Another recent breakthrough for tracing C flow in the rhizosphere is stable isotope probing (SIP). In this technique, isotopically labeled plant assimilates are released into the soil and then subsequently taken up and incorporated into the soil microbial community. The isotopically labeled microbial DNA, RNA or phospholipids can then be extracted and their isotope ratio determined whilst genetic material can be sequenced to identify members of the soil microbial community consuming the rhizodeposits (Singh et al. 2004, Rangel-Castro et al. 2005a, b; Shrestha et al. 2008). However, labeling of photoassimilates often requires a sophisticated experimental set-up particularly for large plants (Warembourg and Kummerow 1991). In the case of ^{14}C, its use may be problematic, particularly in the field, due to safety and environmental concerns. This severely limits isotopic investigations on field-grown plants over their entire life cycle (unless ^{13}C pulse-labelling is used, Högberg et al. 2008). Ultimately, this represents a serious concern when calculating agro- or natural-ecosystem C budgets and the potential contribution of rhizodeposition to C sequestration. The use of natural abundance of the stable isotope ^{13}C can provide an elegant alternative (i.e. $\delta^{13}C$; Ekblad and Hogberg 2001). Growing a C_4 plant on a C_3 history soil (and vice versa) allows the tracing of new plant-derived C from the C_4-plant in soil because of the difference in ^{13}C natural abundance in plant material between C_3 and C_4 vegetation (Boutton 1996; Rochette et al. 1999). However, this approach is restricted to limited contexts, typically to

maize grown on a C_3 soil because of the difficulty to find a soil with a known C_3 or C_4 history (Balesdent and Balabane 1992; Qian et al. 1997). Non-isotopic approaches for quantifying rhizodeposition are available using a range of microbial biosensors. These have been employed as semi-quantitative measures of total root C flow and more recently for spatially localising the release of specific exudate components (Paterson et al. 2006).

One major difficulty when attempting to quantify the transfer of labeled C below ground is the mineralization of rhizodeposits by rhizosphere microorganisms. Typically, low molecular weight (MW) root exudates are believed to only have a residence time of a few hours in soil solution as they are rapidly consumed by the C-limited rhizosphere microbial community (Nguyen and Guckert 2001; van Hees et al. 2005). However, as it was observed for glucose, the microbial uptake of substrate and its subsequent mineralization may be decoupled in time. Therefore, the turnover of low molecular weight exudates in soil solution as determined from the kinetics of mineralization are likely to be underestimated by an order of magnitude, indicating turnover times of minutes rather than hours (Hill et al. 2008). Although higher MW rhizodeposits have a slightly longer persistence time in soil, they are still mineralized within a few days (Mary et al. 1992, 1993; Nguyen et al. 2008). This rapid biodegradation of rhizodeposits means that a significant proportion of the rhizodeposits are quickly lost from the soil as labeled CO_2 (rhizomicrobial respiration). The longer the labeling and the chase period, the greater the amounts of rhizodeposits are lost in this way. Because a large proportion of the rhizodeposits are low MW and labile, rhizomicrobial respiration overlaps directly in time and space with root/symbiont respiration of the same labeled photo-assimilates (Dilkes et al. 2004). Experimentally, the flux of labeled CO_2 derived directly from roots and indirectly from rhizodeposits are therefore determined together (rhizosphere respiration; Todorovic et al. 2001). Knowledge of the partitioning of rhizosphere respiration into root, symbiont and rhizomicrobial components, however, is crucial if we are to gain a deeper understanding of rhizosphere C flow (Paterson 2003; Paterson et al. 2005). Many attempts have been made to partition rhizosphere respiration, from the simple use of antibiotics to more sophisticated models based on isotopic methods, however, none has proved satisfactory from a quantitative perspective (Cheng et al. 1993; Kuzyakov 2006; Sapronov and Kuzyakov 2007). Current estimates suggest that approximately 50% of rhizosphere respiration is due to the turnover of rhizodeposits and 50% to direct root (and mycorrhizal) respiration, however, it is clear that this needs to be major focus for research in the future (Kuzyakov 2002).

Estimating N rhizodeposition in soil is commonly undertaken with a ^{15}N isotopic tracer (Hertenberger and Wanek 2004). The tracer is supplied by a foliar application as a solution or spray, by stem feeding, by a pre-culture on a labeled substrate or by using split-root systems, one compartment for being used for the labeling and the other for determining the release of ^{15}N from roots (Jensen 1996; Hogh-Jensen and Schjoerring 2001; Mayer et al. 2003). All methods currently assume, (1) a homogenous mixing of the tracer within the plant N pool, and (2) that the isotopic signature of N-rhizodeposits is the same as that of the roots. Further rigorous validation of these assumptions is required. Depending on the soil conditions, a fraction of the rhizodeposited ^{15}N also may be unrecovered due to denitrification leading to an underestimation of N rhizodeposition (de Graaff et al. 2007). Recent advances have also been made in the dual ^{13}C-^{15}N isotopic labeling of plants in situ (Wichern et al. 2007).

To overcome the difficulties related to non-sterile soil conditions, many studies were and are still conducted in sterile hydroponic culture. Under these conditions both the amount and the nature of compounds released from roots can be determined. However, one has to be aware of the limitations of such experimental conditions. For instance, both the nature and quantity of compounds released from roots depends on the plant/root physiology, which greatly differs between a simple sterile nutrient solution and a complex soil environment (Neumann and Römheld 2001). Furthermore, exudation has been quantified for decades in nutrient solution which are not regularly renewed, a system that exacerbates the re-uptake of exudates by roots and that leads to a large underestimation in exudation rates (Jones and Darrah 1993). Consequently, it is necessary to adapt the experimental set-up used to study exudation so that it account for the re-uptake of exudates. This can be done by using microcosms percolated by nutrient solution (Hodge et al. 1996) or by modelling the kinetics of

exudate accumulation in the root bathing solution as the net output between the gross efflux and the re-uptake of exudates (Personeni et al. 2007). The use of bioreporter microorganisms is also an interesting approach to spatially localize the release of some specific compounds or class of compounds, however, quantitative information about the rhizodeposition flux are difficult to achieve (Yeomans et al. 1999; Darwent et al. 2003).

Investigations of rhizodeposition are hampered by many technical difficulties and sometimes by unresolved methodological problems arising from the numerous interactions between roots, the soil matrix and microorganisms (van Hees et al. 2005). Availability of robust methodologies for the qualitative and quantitative determination of rhizodeposition in soil clearly remains an unsolved issue. Current methods are often incomplete or biased and consequently, estimates of the flux of C (and to a lesser extend of N) to the rhizosphere are associated with significant uncertainty.

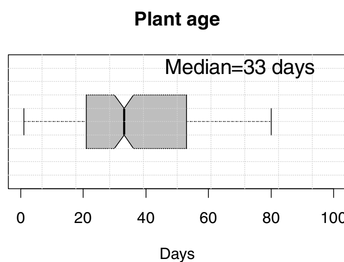
How much C is lost via rhizodeposition?

In the last few decades, hundreds of attempts have been made to quantify the amount of photoassimilate C partitioned below ground (Nguyen 2003). Most of the initial studies used ^{14}C although ^{13}C is now increasingly being used for tracing purposes. Results are commonly expressed as partition coefficients describing that amount of net fixed C allocated between shoots, roots, rhizosphere respiration (root and symbiont respiration + respiration of rhizodeposits) and soil residues. Soil residues include rhizodeposits, microbial biomass-C and metabolites derived from rhizodeposits (including mycorrhizal hyphae) but also fine roots debris that cannot be effectively separated from the soil (e.g. root hairs, epidermal cells etc). Figure 5 summarizes a review of whole plant C partitioning averaged across a wide range of published studies and updates previous reviews (Bidel et al. 2000; Nguyen 2003). Overall, it is clear that most isotopic labeling studies have focussed on young plants at a vegetative stage (typically <1 month old). The focus on young plants is due to methodological difficulties in growing and labeling plants to maturity in controlled conditions. However, plant age has a strong effect of the partitioning of photoassimilate to the rhizosphere. For example, in annual plants pulse-labelled with ^{14}C, when comparing two plant ages ranging within the range 28–600 days of culture, the partitioning of C to rhizosphere clearly decreases with plant age of −43%, −28%, −20% for roots, rhizosphere respiration and soil residues, respectively (median values; Nguyen 2003). Although C partitioning has been investigated in a wide range of plant species, almost half of the published data are for wheat and rye-grass and 76% of the studies are related to five crop/grassland species. Hence, we currently have a very incomplete picture of C rhizodeposition particularly in mixed plant communities. In particular, dicotyledonous plants have received little attention and the amount of rhizodeposition by trees in natural ecosystems remains virtually unknown with the exception of recent studies by (Högberg et al. 2008). Furthermore, when very young trees have been used to study rhizodeposition, the experimental conditions employed often bear little relevance to natural forest stands. Consequently, our poor knowledge of rhizodeposition in trees is problematic, particularly when quantifying C sequestration in forests.

Studies indicate that roughly 40% of net fixed C is allocated belowground. For cereals and grasses, this approximates to around 1.5–2.2 t C ha^{-1} for the vegetation period (Kuzyakov and Domanski 2000). Of the C partitioned below ground about 50% of it is retained in root biomass (19% of net fixed C), 33% is returned to the atmosphere as rhizosphere respiration (12% of net fixed C), 12% can be recovered as soil residues (5% of net fixed C) and a small amount is lost by leaching and surface runoff. Assuming that roots and microorganisms contribute equally to rhizosphere respiration (Kuzyakov 2006), an assumption that must be treated with caution, then a rough estimate of rhizodeposition would be around 11% of the net fixed C or 27% of C allocated to roots. This would correspond to 400–600 kg C ha^{-1} for the vegetation period of grasses and cereals. These values only provide a rough estimate, however, due to the uncertainty surrounding the partitioning of rhizosphere respiration and because soil residues often include small roots and living mycorrhizal mycelium that cannot be realistically separated from soil by current protocols. This probably explains the skewed distribution of the soil residue partitioning coefficients (Fig. 5).

Studies quantifying the amount of N rhizodeposition are much less numerous and a survey of the

Species	Number of partitioning coefficient sets	% of total
Triticum aestivum	75	27.7
Lolium perenne	55	20.3
Bromus erectus	28	10.3
Hordeum vulgare	26	9.6
Zea mays	23	8.5
Avena sativa	9	3.3
Bromus madritensis	8	3.0
Castanea sativa	8	3.0
Salix viminalis	5	1.8
Trifolium repens	5	1.8
Festuca arundinacea	4	1.5
Pinus taeda	4	1.5
Populus tremuloides	4	1.5
Brassica napus	3	1.1
Festuca pratensis	3	1.1
Cynodon dactylon	2	0.7
Lolium multiflorum	2	0.7
Lycopersicon esculent	2	0.7
Medicago truncatula	2	0.7
Pisum sativum	2	0.7
Bouteloua gracilis	1	0.4
Total	271	100



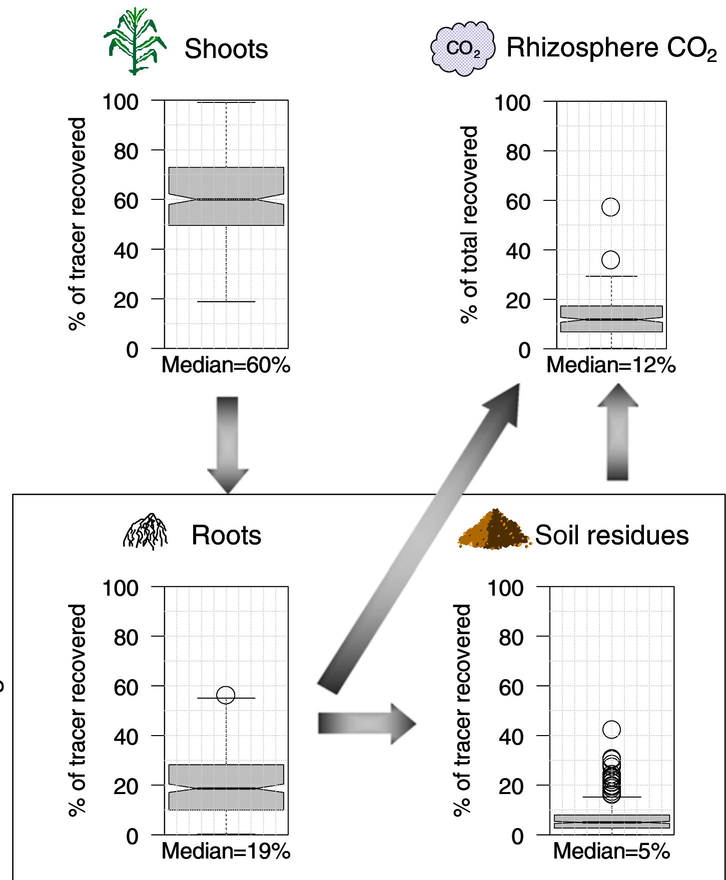


Fig. 5 Partitioning of labeled net fixed C after a pulse or continuous exposure of shoots to a $^{14}CO_2$ enriched atmosphere. For each compartment, *boxplots* show the distribution of 271 individual partition coefficients drawn from a review of the literature by Nguyen (2003) and updated to 2007. The plant species and the distribution of plant ages are provided on the *left*. The *box* represents the second and third quartiles separated by the median. The *whiskers* extend to 1.5 times the interquartile range. The *circles* denote outliers

literature shows that our knowledge of this phenomenon is very incomplete (Fig. 6). More than 60% of the available data pertain to pea and wheat. In these studies, N rhizodeposition accounts for 10–16% of total plant N with losses higher in legumes in comparison to non-legume species. This observation may be biased, however, as the legume based studies have tended to use older plants (Fig. 6) where a larger part of rhizodeposited N may be attributed to root turnover. As free amino acids and proteins represent only a minor component of root exudates (typically 1–2% of exudate-C; Kraffczyk et al. 1984; Jones and Darrah 1993) we assume that they contribute little to plant N rhizodeposition. We conclude that N rhizodeposition must be largely due to root turnover or possibly to an efflux of labeled ammonium and/or nitrate (Feng et al. 1994; Scheurwater et al. 1999). Small root debris that cannot be separated by common sampling protocols may also lead to an overestimation of N rhizodeposition.

Published reports also show that the partition coefficients of C and N both below ground and to rhizodeposition are highly variable. This illustrates that plant species, plant ecotype/cultivar, age and environmental conditions all exert a strong impact on rhizodeposition. From conventional tracer experiments it is often difficult to conclude about how rhizodeposition is affected by environmental conditions as the partitioning of rhizosphere respiration between the root and the microbial components may also be altered. However, when the partitioning of C to root, to rhizosphere respiration and to soil residues changes in the same way, some conclusions may be drawn. Hence, it can be assumed that the percentage

Species	Number of results	% of total
Avena sativa	3	4.0
Cajanus cajan	1	1.3
Cicer arietinum	1	1.3
Glycine max	1	1.3
Hordeum vulgare	2	2.7
Lathyrus sativus	1	1.3
Lolium perenne	1	1.3
Lupinus albus	1	1.3
Lupinus angustifolius	1	1.3
Medicago sativa	1	1.3
Ornithopus compressus	1	1.3
Pisum sativum	27	36.0
Trifolium pratense	1	1.3
Trifolium pratense	1	1.3
Trifolium repens	2	2.7
Trifolium subterraneum	1	1.3
Triticum aestivum	20	26.7
Triticum turgidum	6	8.0
Vicia faba	2	2.7
Vigna radiata	1	1.3
Total	75	100

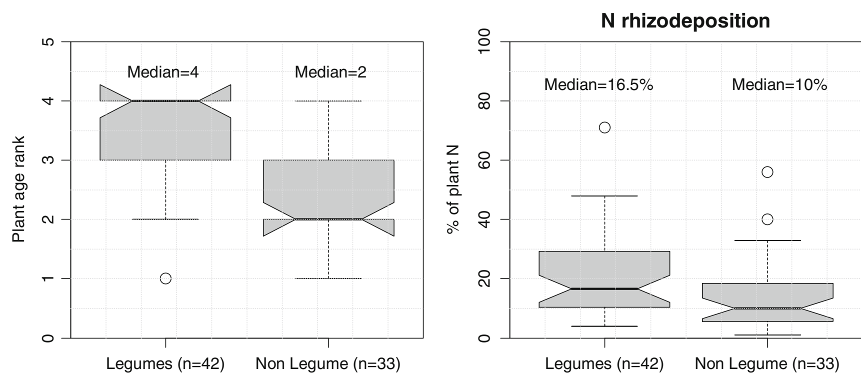


Fig. 6 Summary of published studies on N rhizodeposition expressed as a percentage of total plant N. Rhizosphere N derived from roots was determined by labeling of plant N with ^{15}N supplied as $^{15}NH_3$, $^{15}NO_3$ or ^{15}N-urea. The technique used was one of the following: split-root cultures, stem/petiole infiltration/injection, leaf dipping, $^{15}NH_3$-enriched atmosphere or preculture on a ^{15}N-labelled substrate. The plant species and the ranked distribution of plant age are given on the *left*. Ranks for plant ages are defined as follows: *1* early vegetative stage, *2* end of vegetative stage, *3* flowering/grain filling, *4* maturity. The *box* represents the second and third quartiles separated by the median. The *whiskers* extend to 1.5 times the interquartile range. *Circles* represent outliers

of assimilates ending up as rhizodeposition generally decreases with plant age and is increased by the presence of microorganisms and by elevated atmospheric CO_2.

We now have almost 30 years of knowledge from C rhizodeposition research. From tracer experiments, we can reasonably predict the order of magnitude of this C flux for agroecosystems. These studies all attest to rhizodeposition being a major C flux. In hindsight, however, it is also evident that a quantitative approach to assessing the functional role of rhizodeposition in soil is strongly limited by technical difficulties arising from the complex interactions occurring in the rhizosphere and the tight link between rhizodeposition and the plant's physiological status. Accordingly, there is an urgent need to develop new approaches and methods for probing rhizodeposition. The coupling of plant labeling with molecular tools is promising for understanding the link between the plant-derived C and microbial processes in the rhizosphere but the current information remains more qualitative than quantitative. Considering the need to have a quantitative understanding of C and N fluxes in the rhizosphere to predict ecosystem behaviour, modelling approaches should be considered to be of major importance. For example, integrated modelling of rhizosphere functioning could help to assess previous estimates of rhizodeposition by cross validation of rhizodeposition models with other models, for which the output variables are tightly connected to rhizodeposition and are more accessible (e.g. microbial growth, N dynamics). This could help to integrate our knowledge, to link rhizodeposition with plant functioning and to upscale case studies to the ecosystem level.

Modelling approaches

Mathematical modelling has the potential to predict C flows at spatial and temporal scales that are beyond the capability of current experimental techniques (Darrah et al. 2006). The construction and use of these models, however, are only as good as the knowledge of the individual processes and the values they are parameterized with. We know that the rhizosphere is inherently complex and that by default, current mathematical models are highly simplistic from a mechanistic standpoint. Despite this, however, there is also no doubt that they have greatly improved our understanding of rhizosphere processes (Barber 1995; Nye and Tinker 2000). In addition, it is also clear that major advances in mathematically describ-

ing the complexity of the rhizosphere have been made in recent years (Roose and Fowler 2004; Schnepf and Roose 2006). These advances have been only become possible through interdisciplinary interaction between applied mathematicians and rhizosphere biologists.

In a rhizodeposition context, one of the first quantitative modelling approaches was that taken by Newman and Watson (1977) where rhizosphere C flow was used to drive a soil microbial growth model. This model was subsequently refined by Darrah (1991a, b) with microbial growth placed in a growing root context. In terms of whole plant modelling, a photosynthesis model was used to calculate the flux of C entering the soil using photoassimilate partition coefficients (Swinnen 1994). However, due to the tight relationship between rhizodeposition and plant physiology, the input of C into the soil is not a constant part of the net fixed C or even of the C allocated to roots (see above). Therefore, it is necessary to have a more mechanistical approach, by modelling rhizodeposition along with plant physiology and more particularly with root system functioning. Indeed, exudation, which is a major component of rhizodeposition, is dependent upon root surface area and on the C concentration in root tissue relative to that in the soil solution. Subsequently, exudation can be simplistically modelled by a diffusion equation placed in a vegetation model that simulates plant phenology, canopy assimilation and carbohydrate partitioning above and belowground (Grant 1993). Due to the higher rates of exudation at root apices (McCully and Canny 1985; Darwent et al. 2003), the number and type of lateral branching is an important characteristic to be considered (Henry et al. 2005). Figure 7 shows an example of how this can be done. Exudation of an individual root was modelled from the root surface area (given by the root length and diameter) and by including the longitudinal variability of the C efflux (Personeni et al. 2007). Upscaling this model to the whole root system was achieved by coupling the exudation model to a root architecture model that simulates root emergence, their length and diameter as a function of thermal time (Pages and Pellerin 1996). When this was done the simulated cumulative exudation was 4.9 g C plant^{-1} or 390 kg C ha^{-1} (eight plant m^{-2}) at 860 growing degree days (flowering). This estimate accounts for the longitudinal variability of C efflux along individual roots, for the number of branches and for the root surface area of a model maize root system. This value is consistent with rhizodeposition estimates from tracer experiments, provided that rhizodeposition includes not only exudation but also mucilage, border cells and lysed cells.

There is great interest in coupling the modelling of rhizodeposition with root architecture models as it allows users to simulate changes in rhizodeposition in response to environmental conditions or photoassimilate availability through modifications of the characteristics of the root system. For example, N availability commonly increases root branching and consequently the number of root apices with higher rates of exudation. Similarly, limitation in C allocation to roots induces a reduction in root branching and in root diameter (Thaler and Pages 1998; Bidel et al. 2000)

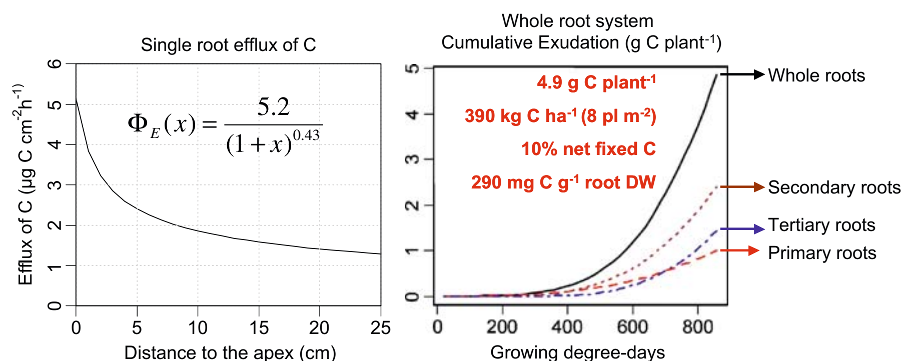


Fig. 7 Modelling of root exudation in maize. *Left*: Experimentally parameterized efflux profile of C from a single root (from Personeni et al. 2007). *Right*: Mathematical simulation of whole root system exudation in maize from germination until flowering (860 growing degree days, base 6°C). The simulation was performed by coupling the single root efflux of C model to the root architecture model of Pages and Pellerin (1996)

and consequently exudation. Furthermore, recent root architecture models have also included C availability in root tissue (Thaler and Pages 1998; Bidel et al. 2000), which is potentially important for modelling diffusive losses. Therefore, further investigations are needed to elucidate if a change in rhizodeposition occurring in response to a modification in photo-assimilate availability (Dilkes et al. 2004) is related to changes in root architecture and/or to changes in C availability within root tissues, which would change the rhizodeposition by individual roots. Much work has yet to be done to understand the mechanisms of N release from roots but a similar approach to that presented for C can be considered to model rhizodeposition of N in relation to the root system structure and functioning. Hence, modelling rhizodeposition with root architecture models that integrate C and N availability in root tissue is undoubtedly a promising perspective for predicting the release of C and N by roots under various environmental conditions.

Rhizodeposition—future outlook

It is clear from the previous discussion that we have made great progress in highlighting the importance of rhizosphere C flow in numerous aspects of ecosystem functioning. However, it is also apparent that we have a very long way to go before we can realistically harness the full extent of this knowledge for landscape level management (e.g. forest sustainability, biodiversity enhancement etc). This is exemplified by our process level understanding of C and nutrient flow at the single root level, however, how this scales up in landscapes which contain a mosaic of hydrologically interconnected vegetation and soil types remains unknown. This is certainly a goal which will only occur through an integration and enhancement of mathematical model scaling techniques. Indeed, the rhizosphere can be expected to play a major role in all the major challenges facing the planet including greenhouse gas mitigation, sustainable food production and food security, bioenergy production, preservation of water quality, accelerated restoration of post-industrial sites etc. One of the major obstacles to achieving this is the shear complexity of the rhizosphere and the lack of experimental techniques for teasing apart the myriad of interactions between roots and their biological, chemical and physical environment. While our knowledge of rhizodeposition has focused on crop plants, for both practical and economic reasons, there is a critical need to assess rhizosphere C flow in complex plant communities. A broader understanding of rhizosphere responses throughout the plant world can yield great insights into plant–soil functioning which cannot be provided by working on crop plants alone (Lambers et al. 2008). Similarly, there is also a need to look at rhizosphere processes in mature trees and particularly in mixed plantations where many synergistic relationships have been reported to occur (e.g. in litter decomposition, mycorrhizal interactions etc; Rothe and Binkley 2001). With the ongoing advances in our experimental and theoretical understanding of plant and microbial genomics, proteomics and metabolomics and the current focus on systems biology (Meldrum 2000), it is evident that rhizodeposition will remain a major focus of research for the foreseeable future. This increase in technology inevitably brings new challenges. In particular, finding robust statistical approaches to disentangle massive datasets produced from temporal and spatial sampling will be a necessity to maximise the potential of the technology (e.g. those produced by biodiversity measures such as pyrosequencing; Emerson et al. 2008; Fulthorpe et al. 2008). Consequently, rhizosphere bioinformatics is likely to grow in importance in the next decade. One of the most promising areas for further development is manipulating rhizosphere C flow to produce sustainable agricultural production systems. If we can interpret the C signals in the rhizosphere and then manipulate their flow, there is a potential to influence rhizosphere development. This could help to reduce our reliance on pesticides if we can stimulate and preserve the activity of biocontrol agents in the rhizosphere. However, a note of caution must also be made in our attempts to manipulate rhizosphere C flow. Although there are many researchers around the world attempting to alter rhizodeposition to help reduce our over-reliance on chemical fertilizers and pesticides, we must be careful not to over-mine or exploit the natural resources to a point at which the soils are left in a highly degraded state (i.e. unsuitable for colonization by native plants by excessively stripping the soil P pool). Consequently, there is also a pressing need for a debate on the ethics of manipulating the rhizosphere if we want to preserve public support for our research.

Acknowledgements The authors would like to address special thanks to L. Pagès (INRA, Avignon) for providing simulations from root architecture models.

References

Abuzinadah RA, Read DJ (1989) Carbon transfer associated with assimilation of organic nitrogen sources by silver birch (*Betula pendula* Roth.). Trees (Berl) 3:17–23 doi:10.1007/BF00202396

Ahonen-Jonnarth U, Van Hees PAW, Lundström US, Finlay RD (2000) Production of organic acids by mycorrhizal and non-mycorrhizal *Pinus sylvestris* L. seedlings exposed to elevated concentrations of aluminium and heavy metals. New Phytol 146:557–567 doi:10.1046/j.1469-8137.2000.00653.x

Allard V, Robin C, Newton PCD, Lieffering M, Soussana JF (2006) Short and long-term effects of elevated CO_2 on *Lolium perenne* rhizodeposition and its consequences on soil organic matter turnover and plant N yield. Soil Biol Biochem 38:1178–1187 doi:10.1016/j.soilbio.2005.10.002

Amiro BD, Ewing LL (1992) Physiological conditions and uptake of inorganic ^{14}C by plant–roots. Environ Exp Bot 32:203–211 doi:10.1016/0098-8472(92)90003-K

Andersson P, Berggren D (2005) Amino acids, total organic and inorganic nitrogen in forest floor soil solution at low and high nitrogen input. Water Air Soil Pollut 162:369–384 doi:10.1007/s11270-005-7372-y

Antunes PM, Rajcan I, Goss MJ (2006) Specific flavonoids as interconnecting signals in the tripartite symbiosis formed by arbuscular mycorrhizal fungi, *Bradyrhizobium japonicum* (Kirchner) Jordan and soybean (*Glycine max* (L.) Merr.). Soil Biol Biochem 38:533–543 doi:10.1016/j.soilbio.2005.06.008

Bacic A, Moody SF, McComb JA, Hinch JM, Clarke AE (1987) Extracellular polysaccharides from shaken liquid cultures of *Zea mays*. Aust J Plant Physiol 14:633–641

Bahyrycz A, Konopinska D (2007) Plant signalling peptides: some recent developments. J Pept Sci 13:787–797 doi:10.1002/psc.915

Bais HP, Park SW, Weir TL, Callaway RM, Vivanco JM (2004) How plants communicate using the underground information superhighway. Trends Plant Sci 9:26–32 doi:10.1016/j.tplants.2003.11.008

Balesdent J, Balabane M (1992) Maize root-derived soil organic-carbon estimated by natural ^{13}C abundance. Soil Biol Biochem 24:97–101 doi:10.1016/0038-0717(92)90264-X

Barber SA (1995) Soil nutrient bioavailability. Wiley, New York

Bardgett RD, Streeter TC, Bol R (2003) Soil microbes compete effectively with plants for organic-nitrogen inputs to temperate grasslands. Ecology 84:1277–1287 doi:10.1890/0012-9658(2003)084[1277:SMCEWP]2.0.CO;2

Barlow PW (1975) The root cap. In: Torrey JG, Clarkson DT (ed) The development and function of roots (Third Cabot Symposium). Academic, London, pp 21–54

Beemster GTS, Baskin TI (1998) Analysis of cell division and elongation underlying the developmental acceleration of root growth in *Arabidopsis thaliana*. Plant Physiol 116:1515–1526 doi:10.1104/pp.116.4.1515

Bending GD, Read DJ (1995) The structure and function of the vegetative mycelium of ectomycorrhizal plants. V. The foraging behaviour of ectomycorrhizal mycelium and the translocation of nutrients from exploited organic matter. New Phytol 130:401–409 doi:10.1111/j.1469-8137.1995.tb01834.x

Bengough AG, Kirby JM (1999) Tribology of the root cap in maize (*Zea mays*) and peas (*Pisum sativum*). New Phytol 142:421–425 doi:10.1046/j.1469-8137.1999.00406.x

Bengough AG, McKenzie BM (1997) Sloughing of root cap cells decreases the frictional resistance to maize (*Zea mays* L.) root growth. J Exp Bot 48:885–893 doi:10.1093/jxb/48.4.885

Bidartondo MI (2005) The evolutionary ecology of mycoheterotrophy. New Phytol 167:335–352 doi:10.1111/j.1469-8137.2005.01429.x

Bidartondo MI, Redecker D, Hijri I, Wiemken A, Bruns TD, Domínguez L, Sérsic A, Leake JR, Read DJ (2002) Epiparasitic plants specialized on arbuscular mycorrhizal fungi. Nature 419:389–392 doi:10.1038/nature01054

Bidel LPR, Pages L, Riviere LM, Pelloux G, Lorendeau JY (2000) MassFlowDyn I: A carbon transport and partitioning model for root system architecture. Ann Bot (Lond) 85:869–886 doi:10.1006/anbo.2000.1149

Bockenhoff A, Prior DAM, Grundler FMW, Oparka KJ (1996) Induction of phloem unloading in *Arabidopsis thaliana* roots by the parasitic nematode *Heterodera schachtii*. Plant Physiol 112:1421–1427 doi:10.1104/pp.112.4.1421

Boddy E, Hill PW, Farrar J, Jones DL (2007) Fast turnover of low molecular weight components of the dissolved organic carbon pool of temperate grassland field soils. Soil Biol Biochem 39:827–835 doi:10.1016/j.soilbio.2006.09.030

Boutton TW (1996) Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. In: Boutton TW, Yamasaki S (eds) Mass spectrometry of soils. Marcel Dekker, New York, pp 47–82

Bouwmeester HJ, Roux C, Lopez-Raez JA, Bécard G (2007) Rhizosphere communication of plants, parasitic plants and AM fungi. Trends Plant Sci 12:224–230 doi:10.1016/j.tplants.2007.03.009

Brigham LA, Woo H, Nicoll SM, Hawes MC (1995) Differential expression of proteins and mRNAs from border cells and root tips of pea. Plant Physiol 109:457–463

Brown ME (1972) Plant-growth substances produced by microorganisms of soil and rhizosphere. J Appl Bacteriol 35:443–451

Buer CS, Muday GK, Djordjevic MA (2007) Flavonoids are differentially taken up and transported long distances in Arabidopsis. Plant Physiol 145:478–490 doi:10.1104/pp.107.101824

Canny MJ (1995) Apoplastic water and solute movement—new rules for an old space. Annu Rev Plant Physiol Plant Mol Biol 46:215–236 doi:10.1146/annurev.pp.46.060195.001243

Chapin FS, Moilanen L, Kielland K (1993) Preferential use of organic nitrogen for growth by a nonmycorrhizal arctic sedge. Nature 361:150–153 doi:10.1038/361150a0

Cheng WX, Coleman DC, Carroll CR, Hoffman C (1993) In-situ measurement of root respiration and soluble C-concentrations in the rhizosphere. Soil Biol Biochem 25:1189–1196 doi:10.1016/0038-0717(93)90251-6

Ciereszko I, Farrar JF, Rychter AM (1999) Compartmentation and fluxes of sugars in roots of *Phaseolus vulgaris* under phosphate deficiency. Biol Plant 42:223–231 doi:10.1023/A:1002108601862

Clark FE (1949) Soil microorganisms and plant roots. Adv Agron 1:241–288 doi:10.1016/S0065-2113(08)60750-6

Cram WJ (1974) Effects of Cl^{-} on HCO_3^{-} and malate fluxes and CO_2 fixation in carrot and barley root cells. J Exp Bot 25:253–268 doi:10.1093/jxb/25.2.253

Curl EA, Truelove (1986) The rhizosphere. Advanced series in agricultural science 15. Springer, Berlin

Czarnes S, Hallett PD, Bengough AG, Young IM (2000) Root- and microbial-derived mucilages affect soil structure and water transport. Eur J Soil Sci 51:435–443 doi:10.1046/j.1365-2389.2000.00327.x

Dakora FD, Phillips DA (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245:35–47 doi:10.1023/A:1020809400075

Darrah PR (1991a) Models of the rhizosphere. 1. Microbial-population dynamics around a root releasing soluble and insoluble carbon. Plant Soil 133:187–199 doi:10.1007/BF00009191

Darrah PR (1991b) Models of the rhizosphere. 2. A quasi 3-dimensional simulation of the microbial-population dynamics around a growing root releasing soluble exudates. Plant Soil 138:147–158 doi:10.1007/BF00012241

Darrah PR, Jones DL, Kirk GJD, Roose T (2006) Modelling the rhizosphere: a review of methods for 'upscaling' to the whole-plant scale. Eur J Soil Sci 57:13–25 doi:10.1111/j.1365-2389.2006.00786.x

Darwent MJ, Paterson E, McDonald AJS, Tomos AD (2003) Biosensor reporting of root exudation from *Hordeum vulgare* in relation to shoot nitrate concentration. J Exp Bot 54:325–334 doi:10.1093/jxb/54.381.325

de Graaff MA, Six J, van Kessel C (2007) Elevated CO_2 increases nitrogen rhizodeposition and microbial immobilization of root-derived nitrogen. New Phytol 173:778–786 doi:10.1111/j.1469-8137.2006.01974.x

Derrien D, Marol C, Balesdent J (2004) The dynamics of neutral sugars in the rhizosphere of wheat. An approach by ^{13}C pulse-labelling and GC/C/IRMS. Plant Soil 267:243–253 doi:10.1007/s11104-005-5348-8

Dilkes NB, Jones DL, Farrar J (2004) Temporal dynamics of carbon partitioning and rhizodeposition in wheat. Plant Physiol 134:706–715 doi:10.1104/pp.103.032045

Dilworth MJ, James EK, Sprent JI, Newton WE (2008) Nitrogen-fixing leguminous symbioses. Springer, New York

Dimou M, Flemetakis E, Delis C, Aivalakis G, Spyropoulos KG, Katinakis P (2005) Genes coding for a putative cell-wall invertase and two putative monosaccharide/H^+ transporters are expressed in roots of etiolated *Glycine max* seedlings. Plant Sci 169:798–804 doi:10.1016/j.plantsci.2005.05.037

DiTomaso JM, Hart JJ, Kochian LV (1992) Transport kinetics and metabolism of exogenously applied putrescine in roots of intact maize seedlings. Plant Physiol 98:611–620 doi:10.1104/pp.98.2.611

Ekblad A, Hogberg 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 doi:10.1007/s004420100667

Eleftheriou EP, Lazarou DS (1997) Cytochemical localization of ATPase activity in roots of wheat (*Triticum aestivum*). Biologia 52:573–583

Emerson D, Agulto L, Liu H, Liu LP (2008) Identifying and characterizing bacteria in an era of genomics and proteomics. Bioscience 58:925–936 doi:10.1641/B581006

Farrar J, Hawes M, Jones D, Lindow S (2003) How roots control the flux of carbon to the rhizosphere. Ecology 84:827–837 doi:10.1890/0012-9658(2003)084[0827:HRCTFO]2.0.CO;2

Faure D, Bloemberg G, Leveau J, Veereecke D (2009) Molecular communications in the rhizosphere. Plant Soil (this volume)

Feng JN, Volk RJ, Jackson WA (1994) Inward and outward transport of ammonium in roots of maize and sorghum—contrasting effects of methionine sulfoximine. J Exp Bot 45:429–439 doi:10.1093/jxb/45.4.429

Filion M, St-Arnaud M, Fortin JA (1999) Direct interaction between the arbuscular mycorrhizal fungus *Glomus intraradices* and different rhizosphere micro-organisms. New Phytol 141:525–533 doi:10.1046/j.1469-8137.1999. 00366.x

Finlay RD (2008) Ecological aspects of mycorrhizal symbiosis with special emphasis on the functional diversity of interactions involving the extraradical mycelium. J Exp Bot 59:1115–1126 doi:10.1093/jxb/ern059

Finlay RD, Rosling A (2006) Integrated nutrient cycles in forest ecosystems, the role of ectomycorrhizal fungi. In: Gadd GM (ed) Fungi in biogeochemical cycles. Cambridge University Press, Cambridge, pp 28–50

Finlay R, Söderström B (1992) Mycorrhiza and carbon flow to the soil. In: Allen MJ (ed) Mycorrhizal functioning. Chapman & Hall, New York, pp 134–160

Fischer WN, Andre B, Rentsch D, Krolkiewicz S, Tegeder M, Breitkreuz K, Frommer WB (1998) Amino acid transport in plants. Trends Plant Sci 3:188–195 doi:10.1016/S1360-1385(98)01231-X

Fleischer A, Ehwald R (1995) The free-space of sugars in plant-tissues—external film and apoplastic volume. J Exp Bot 46:647–654 doi:10.1093/jxb/46.6.647

Ford CR, Wurzburger N, Hendrick RL, Teskey RO (2007) Soil DIC uptake and fixation in *Pinus taeda* seedlings and its C contribution to plant tissues and ectomycorrhizal fungi. Tree Physiol 27:375–383

Francis R, Read DJ (1984) Direct transfer of carbon between plants connected by vesicular arbuscular mycorrhizal mycelium. Nature 307:53–56 doi:10.1038/307053a0

Fulthorpe RR, Roesch LFW, Riva A, Triplett EW (2008) Distantly sampled soils carry few species in common. ISME J 2:901–910 doi:10.1038/ismej.2008.55

Fusseder A (1987) The longevity and activity of the primary root of maize. Plant Soil 101:257–265 doi:10.1007/BF02370653

Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Markewitz D, Richter DD (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129:420–429

Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147:13–31 doi:10.1046/j.1469-8137.2000.00681.x

Godbold DL, Hoosbeek MR, Lukac M, Cotrufo MF, Janssens IA, Ceulemans R, Polle A, Velthorst EJ, Scarascia-

Mugnozza G, DeAngelis P, Miglietta F, Peressotti A (2006) Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. Plant Soil 281:15–24 doi:10.1007/s11104-005-3701-6

Gout E, Bligny R, Pascal N, Douce R (1993) ^{13}C nuclear-magnetic-resonance studies of malate and citrate synthesis and compartmentation in higher-plant cells. J Biol Chem 268:3986–3992

Grant RF (1993) Rhizodeposition by crop plants and its relationship to microbial activity and nitrogen distribution. Model Geo-Biosph Process 2:193–209

Grayston SJ, Vaughan D, Jones D (1996) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl Soil Ecol 5:29–56 doi:10.1016/S0929-1393(96)00126-6

Guckert A, Breisch H, Reisinger O (1975) Soil/root interface. 1. Electron microscope study of mucigel/clay micro-organism relations. Soil Biol Biochem 7:241–250 doi:10.1016/0038-0717(75)90061-9

Gunawardena U, Hawes MC (2002) Tissue specific localization of root infection by fungal pathogens: role of root border cells. Mol Plant Microbe Interact 15:1128–1136 doi:10.1094/MPMI.2002.15.11.1128

Hart JJ, DiTomaso JM, Linscott DL, Kochian LV (1992) Transport interactions between paraquat and polyamines in roots of intact maize seedlings. Plant Physiol 99:1400–1405 doi:10.1104/pp.99.4.1400

Hartmann A, Berg G, van Tuinen D (2009) Plant-driven selection of microbes. Plant Soil (this volume)

Hawes MC, Brigham LA, Wen F, Woo HH, Zhu Z (1998) Function of root border cells in plant health: pioneers in the rhizosphere. Annu Rev Phytopathol 36:311–327 doi:10.1146/annurev.phyto.36.1.311

Hawes MC, Gunawardena U, Miyasaka S, Zhao XW (2000) The role of root border cells in plant defence. Trends Plant Sci 5:128–133 doi:10.1016/S1360-1385(00)01556-9

Haydon MJ, Cobbett CS (2007) Transporters of ligands for essential metal ions in plants. New Phytol 174:499–506 doi:10.1111/j.1469-8137.2007.02051.x

Henry F, Nguyen C, Paterson E, Sim A, Robin C (2005) How does nitrogen availability alter rhizodeposition in *Lolium multiflorum* Lam. during vegetative growth? Plant Soil 269:181–191 doi:10.1007/s11104-004-0490-2

Herrmann A, Felle HH (1995) Tip growth in root hair-cells of *Sinapis-alba*. 1—significance of internal and external Ca^{2+} and pH. New Phytol 129:523–533 doi:10.1111/j.1469-8137.1995.tb04323.x

Hertenberger G, Wanek W (2004) Evaluation of methods to measure differential ^{15}N labeling of soil and root N pools for studies of root exudation. Rapid Commun Mass Spectrom 18:2415–2425 doi:10.1002/rcm.1615

Hill PW, Marshall C, Williams GG, Blum H, Harmens H, Jones DL, Farrar JF (2007) The fate of photosynthetically-fixed carbon in *Lolium perenne* grassland as modified by elevated CO_2 and sward management. New Phytol 173:766–777 doi:10.1111/j.1469-8137.2007.01966.x

Hill PW, Farrar JF, Jones DL (2008) Decoupling of microbial glucose uptake and mineralization in soil. Soil Biol Biochem 40:616–624 doi:10.1016/j.soilbio.2007.09.008

Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237:173–195 doi:10.1023/A:1013351617532

Hinsinger P, Bengough AG, Vetterlein D, Young IM (2009) Rhizosphere: biophysics, biogeochemistry and ecological relevance. Plant Soil (this volume)

Hirner A, Ladwig F, Stransky H, Okumoto S, Keinath M, Harms A, Frommer WB, Koch W (2006) Arabidopsis LHT1 is a high-affinity transporter for cellular amino acid uptake in both root epidermis and leaf mesophyll. Plant Cell 18:1931–1946 doi:10.1105/tpc.106.041012

Hodge A, Grayston SJ, Ord BG (1996) A novel method for characterisation and quantification of plant root exudates. Plant Soil 184:97–104 doi:10.1007/BF00029278

Hodge A, Paterson E, Thornton B, Millard P, Killham K (1997) Effects of photon flux density on carbon partitioning and rhizosphere carbon flow of *Lolium perenne*. J Exp Bot 48:1797–1805

Hodge A, Campbell CD, Fitter AH (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature 413:297–299 doi:10.1038/35095041

Hoffland E, Findenegg GR, Nelemans JA (1989) Solubilization of rock phosphate by rape. 2. Local root exudation of organic-acids as a response to P-starvation. Plant Soil 113:161–165 doi:10.1007/BF02280176

Högberg MN, Högberg P (2002) Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytol 154:791–795 doi:10.1046/j.1469-8137.2002.00417.x

Högberg P, Read DJ (2006) Towards a more plant physiological perspective on soil ecology. Trends Ecol Evol 21:548–554 doi:10.1016/j.tree.2006.06.004

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792 doi:10.1038/35081058

Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell C, Schindlbacher A, Hurry V, Lundmark T, Linder S, Näsholm T (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytol 177:220–228

Hogh-Jensen H, Schjoerring JK (2001) Rhizodeposition of nitrogen by red clover, white clover and ryegrass leys. Soil Biol Biochem 33:439–448 doi:10.1016/S0038-0717(00)00183-8

Huang LF, Bocock PN, Davis JM, Koch KE (2007) Regulation of invertase: a suite of transcriptional and post-transcriptional mechanisms. Funct Plant Biol 34:499–507 doi:10.1071/FP06227

Hukin D, Doering-Saad C, Thomas CR, Pritchard J (2002) Sensitivity of cell hydraulic conductivity to mercury is coincident with symplasmic isolation and expression of plasmalemma aquaporin genes in growing maize roots. Planta 215:1047–1056 doi:10.1007/s00425-002-0841-2

Iijima M, Griffiths B, Bengough AG (2000) Sloughing of cap cells and carbon exudation from maize seedling roots in

compacted sand. New Phytol 145:477–482 doi:10.1046/j.1469-8137.2000.00595.x
Iijima M, Higuchi T, Barlow PW (2004) Contribution of root cap mucilage and presence of an intact root cap in maize (*Zea mays*) to the reduction of soil mechanical impedance. Ann Bot (Lond) 94:473–477 doi:10.1093/aob/mch166
Jahn T, Baluska F, Michalke W, Harper JF, Volkmann D (1998) Plasma membrane H^+-ATPase in the root apex: evidence for strong expression in xylem parenchyma and asymmetric localization within cortical and epidermal cells. Physiol Plant 104:311–316 doi:10.1034/j.1399-3054.1998. 1040304.x
Jensen ES (1996) Rhizodeposition of N by pea and barley and its effect on soil N dynamics. Soil Biol Biochem 28:65–71 doi:10.1016/0038-0717(95)00116-6
Jiang K, Zhang SB, Lee S, Tsai G, Kim K, Huang HY, Chilcott C, Zhu T, Feldman LJ (2006) Transcription profile analyses identify genes and pathways central to root cap functions in maize. Plant Mol Biol 60:343–363 doi:10.1007/s11103-005-4209-4
Johansson JF, Paul LR, Finlay RD (2004) Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. FEMS Microbiol Ecol 48:1–13 doi:10.1016/j.femsec.2003.11.012
Johnson JF, Allan DL, Vance CP, Weiblen G (1996) Root carbon dioxide fixation by phosphorus-deficient *Lupinus albus*—contribution to organic acid exudation by proteoid roots. Plant Physiol 112:19–30 doi:10.1104/pp.112.1.31
Johnson D, Leake JR, Ostle N, Ineson P, Read DJ (2002) In situ $^{13}CO_2$ pulse-labelling of upland grassland demonstrates that a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. New Phytol 153:327–334 doi:10.1046/j.0028-646X.2001.00316.x
Johnson D, Krsek M, Wellington EMH, Stott AW, Cole L, Bardgett RD, Read DJ, Leake JR (2005) Soil invertebrates disrupt carbon flow through fungal networks. Science 309:1047 doi:10.1126/science.1114769
Jones DL, Darrah PR (1992) Resorption of organic-components by roots of *Zea mays* L. and its consequences in the rhizosphere. 1. Resorption of ^{14}C labelled glucose, mannose and citric-acid. Plant Soil 143:259–266 doi:10.1007/BF00007881
Jones DL, Darrah PR (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 Soil 153:47–59 doi:10.1007/BF00010543
Jones DL, Darrah PR (1994) Amino-acid influx at the soil–root interface of *Zea mays* L. and its implications in the rhizosphere. Plant Soil 163:1–12
Jones DL, Darrah PR (1995) Influx and efflux of organic-acids across the soil–root interface of *Zea mays* L. and its implications in rhizosphere C flow. Plant Soil 173:103–109 doi:10.1007/BF00155523
Jones DL, Darrah PR (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 Soil 178:153–160 doi:10.1007/BF00011173
Jones DL, Darrah PR, Kochian LV (1996) Critical evaluation of organic acid mediated iron dissolution in the rhizosphere and its potential role in root iron uptake. Plant Soil 180:57–66
Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol 163:459–480 doi:10.1111/j.1469-8137.2004.01130.x
Jones DL, Healey JR, Willett VB, Farrar JF (2005a) Dissolved organic nitrogen uptake by plants—an important N uptake pathway? Soil Biol Biochem 37:413–423 doi:10.1016/j.soilbio.2004.08.008
Jones DL, Shannon D, Junvee-Fortune T, Farrar JF (2005b) Plant capture of free amino acids is maximized under high soil amino acid concentrations. Soil Biol Biochem 37:179–181 doi:10.1016/j.soilbio.2004.07.021
Jun JH, Fiume E, Fletcher JC (2008) The CLE family of plant polypeptide signalling molecules. Cell Mol Life Sci 65:743–755 doi:10.1007/s00018-007-7411-5
Knox OGG, Gupta VVSR, Nehl DB, Stiller WN (2007) Constitutive expression of Cry proteins in roots and border cells of transgenic cotton. Euphytica 154:83–90 doi:10.1007/s10681-006-9272-7
Körner C, Asshoff R, Bignucolo O, Hättenschwiler R, Keel SG, Peláez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309:1360–1362
Kraffczyk I, Trolldenier G, Beringer H (1984) Soluble root exudates of maize: influence of potassium supply and rhizosphere microorganisms. Soil Biol Biochem 16:315–322 doi:10.1016/0038-0717(84)90025-7
Kramer EM, Frazer NL, Baskin TI (2007) Measurement of diffusion within the cell wall in living roots of *Arabidopsis thaliana*. J Exp Bot 58:3005–3015 doi:10.1093/jxb/erm155
Kuzyakov Y (2002) Separating microbial respiration of exudates from root respiration in non-sterile soils: a comparison of four methods. Soil Biol Biochem 34:1621–1631 doi:10.1016/S0038-0717(02)00146-3
Kuzyakov Y (2006) Sources of CO_2 efflux from soil and review of partitioning methods. Soil Biol Biochem 38:425–448 doi:10.1016/j.soilbio.2005.08.020
Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. J Plant Nutr Soil Sci 163:421–431 doi:10.1002/1522-2624(200008)163:4<421::AID-JPLN421>3.0.CO;2-R
Kuzyakov Y, Jones DL (2006) Glucose uptake by maize roots and its transformation in the rhizosphere. Soil Biol Biochem 38:851–860 doi:10.1016/j.soilbio.2005.07.012
Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103 doi:10.1016/j.tree.2007.10.008
Lambers H, Mougel C, Jaillard B, Hinsinger P (2009) Plant–microbe–soil interactions in the rhizosphere: an evolutionary perspective. Plant Soil (this volume)
Lasat MM (2002) Phytoextraction of toxic metals: a review of biological mechanisms. J Environ Qual 31:109–120
Leake JR (2004) Myco-heterotroph/epiparasitic plant interactions with ectomycorrhizal and arbuscular mycorrhizal fungi. Curr Opin Plant Biol 7:422–428 doi:10.1016/j.pbi.2004.04.004
Leake JR, Donnelly DP, Saunders EM, Boddy L, Read DJ (2001) Rates and quantities of carbon flux to ectomycorrhizal mycelium following ^{14}C pulse labeling of *Pinus sylvestris* seedlings: effects of litter patches and interaction with a wood decomposer fungus. Tree Physiol 21:71–82

Leake JR, Johnson D, Donnelly D, Muckle G, Boddy L, Read DJ (2004) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Can J Bot 82:1016–1045 doi:10.1139/b04-060

Leinweber P, Eckhardt KU, Fischer H, Kuzyakov Y (2008) A new rapid micro-method for the molecular–chemical characterization of rhizodeposits by field-ionization mass spectrometry. Rapid Commun Mass Spectrom 22:1230–1234 doi:10.1002/rcm.3463

Ligaba A, Katsuhara M, Ryan PR, Shibasaka M, Matsumoto H (2006) The BnALMT1 and BnALMT2 genes from rape encode aluminum-activated malate transporters that enhance the aluminum resistance of plant cells. Plant Physiol 142:1294–1303 doi:10.1104/pp.106.085233

Lindahl B, Olsson S, Stenlid J, Finlay RD (2001) Effects of resource availability on mycelial interactions and ^{32}P-transfer between a saprotrophic and an ectomycorrhizal fungus in soil microcosms. FEMS Microbiol Ecol 38:43–52 doi:10.1111/j.1574-6941.2001.tb00880.x

Lindahl BD, Finlay RD, Cairney JWG (2005) Enzymatic activities of mycelia in mycorrhizal fungal communities. In: Dighton J, Oudemans P, White J (eds) The fungal community: its organization and role in the ecosystem. Marcel Dekker, New York, pp 331–348

Lindahl BD, Ihrmark K, Boberg J, Trumbore S, Högberg P, Stenlid J, Finlay RD (2007) Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in boreal forests. New Phytol 173:611–620 doi:10.1111/j.1469-8137.2006.01936.x

Lipson D, Nasholm T (2001) The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. Oecologia 128:305–316 doi:10.1007/s004420100693

Lynch JM (1990) The rhizosphere. Wiley, London

Martin JK (1975) ^{14}C-labeled material leached from rhizosphere of plants supplied continuously with $^{14}CO_2$. Soil Biol Biochem 7:395–399 doi:10.1016/0038-0717(75)90056-5

Mary B, Mariotti A, Morel JL (1992) Use of ^{13}C variations at natural abundance for studying the biodegradation of root mucilage, roots and glucose in soil. Soil Biol Biochem 24:1065–1072 doi:10.1016/0038-0717(92)90037-X

Mary B, Fresneau C, Morel JL, Mariotti A (1993) C-cycling and N-cycling during decomposition of root mucilage, roots and glucose in soil. Soil Biol Biochem 25:1005–1014 doi:10.1016/0038-0717(93)90147-4

Matiru VN, Dakora FD (2005) The rhizosphere signal molecule lumichrome alters seedling development in both legumes and cereals. New Phytol 166:439–444 doi:10.1111/j.1469-8137.2005.01344.x

Mayer J, Buegger F, Jensen ES, Schloter M, Hess J (2003) Estimating N rhizodeposition of grain legumes using a ^{15}N in situ stem labelling method. Soil Biol Biochem 35:21–28 doi:10.1016/S0038-0717(02)00212-2

McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic-matter and nitrogen budgets of 2 forested ecosystems. Ecology 63:1481–1490 doi:10.2307/1938874

McCully ME (1999) Roots in soil: unearthing the complexities of roots and their rhizospheres. Annu Rev Plant Physiol Plant Mol Biol 50:695–718 doi:10.1146/annurev.arplant.50.1.695

McCully ME, Boyer JS (1997) The expansion of maize root-cap mucilage during hydration. 3. Changes in water potential and water content. Physiol Plant 99:169–177 doi:10.1111/j.1399-3054.1997.tb03445.x

McCully ME, Canny MJ (1985) Localisation of translocated ^{14}C in roots and root exudates of field-grown maize. Physiol Plant 65:380–392 doi:10.1111/j.1399-3054.1985.tb08661.x

McDougal BM, Rovira AD (1970) Sites of exudation of ^{14}C-labelled compounds from wheat roots. New Phytol 69:999–1002 doi:10.1111/j.1469-8137.1970.tb02479.x

Meharg AA (1994) A critical-review of labeling techniques used to quantify rhizosphere carbon-flow. Plant Soil 166:55–62 doi:10.1007/BF02185481

Meldrum D (2000) Automation for genomics, part two: sequencers, microarrays, and future trends. Genome Res 10:1288–1303 doi:10.1101/gr.157400

Mench M, Morel JL, Guckert A (1987) Metal binding properties of high molecular weight soluble exudates from maize (*Zea mays* L.) roots. Biol Fertil Soils 3:165–169 doi:10.1007/BF00255778

Miyasaka SC, Hawes MC (2001) Possible role of root border cells in detection and avoidance of aluminum toxicity. Plant Physiol 125:1978–1987 doi:10.1104/pp.125.4.1978

Morel JL, Mench M, Guckert A (1986) Measurement of Pb^{2+}, Cu^{2+} and Cd^{2+} binding with mucilage exudates from maize (*Zea mays* L.) roots. Biol Fertil Soils 2:29–34 doi:10.1007/BF00638958

Morel HJL, Guckert A, Plantureux S, Chenu C (1990) Influence of root exudates on soil aggregation. Symbiosis 9:87–91

Morre DJ, Jones DD, Mollenhauer HH (1967) Golgi apparatus mediated polysaccharide secretion by outer root cap cells of *Zea mays*. 1. Kinetics and secretory pathway. Planta 74:286–301 doi:10.1007/BF00384849

Nadelhoffer KJ, Raich JW (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147 doi:10.2307/1940664

Näsholm T, Ekblad A, Nordin A, Giesler R, Högberg M, Högberg P (1998) Boreal forest plants take up organic nitrogen. Nature 392:914–916 doi:10.1038/31921

Negishi T, Nakanishi H, Yazaki J, Kishimoto N, Fujii F, Shimbo K, Yamamoto K, Sakata K, Sasaki T, Kikuchi S, Mori S, Nishizawa NK (2002) cDNA microarray analysis of gene expression during Fe-deficiency stress in barley suggests that polar transport of vesicles is implicated in phytosiderophore secretion in Fe-deficient barley roots. Plant J 30:83–94 doi:10.1046/j.1365-313X.2002.01270.x

Nehls U (2008) Mastering ectomycorrhizal symbiosis: the impact of carbohydrates. J Exp Bot 59:1097–1108 doi:10.1093/jxb/erm334

Neumann G, Römheld V (2001) The release of root exudates as affected by the plant's physiological status. In: Pinton R, Varini Z, Nannipieri P (eds) The rhizosphere. Biochemistry and organic substances at the soil–plant interface. Marcel Dekker, New York, pp 41–93

Newman EI, Watson A (1977) Microbial abundance in rhizosphere—computer-model. Plant Soil 48:17–56 doi:10.1007/BF00015157

Nguyen C (2003) Rhizodeposition of organic C by plants: mechanisms and controls. Agronomie 23:375–396 doi:10.1051/agro:2003011

Nguyen C, Guckert A (2001) Short-term utilisation of C-14-[U] glucose by soil microorganisms in relation to carbon availability. Soil Biol Biochem 33:53–60 doi:10.1016/S0038-0717(00)00114-0

Nguyen C, Froux F, Recous S, Morvan T, Robin C (2008) Net N immobilisation during the biodegradation of mucilage in soil as affected by repeated mineral and organic fertilization. Nutr Cycl Agroecosyst 80:39–47 doi:10.1007/s10705-007-9119-1

Nye PH, Tinker PB (2000) Solute movement in the rhizosphere. Oxford University Press, Oxford

Offre P, Pivato B, Mazurier S, Siblot S, Berta G, Lemanceau P, Mougel C (2008) Microdiversity of Burkholderiales associated with mycorrhizal and nonmycorrhizal roots of *Medicago truncatula*. FEMS Microbiol Ecol 65:180–192 doi:10.1111/j.1574-6941.2008.00504.x

Ohyama T, Ohtake T, Sueyoshi K, Tewari K, Takahashi Y, Ito S, Nishiwaki T, Nagumo Y, Ishii S, Sato T (2009) Nitrogen fixation and metabolism in soybean plants. Nova, Hauppauge

Oksman-Caldentey KM, Inze D (2004) Plant cell factories in the post-genomic era: new ways to produce designer secondary metabolites. Trends Plant Sci 9:433–440 doi:10.1016/j.tplants.2004.07.006

Ostle N, Whiteley AS, Bailey MJ, Sleep D, Ineson P, Manefield M (2003) Active microbial RNA turnover in a grassland soil estimated using a $^{13}CO_2$ spike. Soil Biol Biochem 35:877–885 doi:10.1016/S0038-0717(03)00117-2

Ovecka M, Lang I, Baluska F, Ismail A, Illes P, Lichtscheidl IK (2005) Endocytosis and vesicle trafficking during tip growth of root hairs. Protoplasma 226:39–54 doi:10.1007/s00709-005-0103-9

Owen AG, Jones DL (2001) Competition for amino acids between wheat roots and rhizosphere microorganisms and the role of amino acids in plant N acquisition. Soil Biol Biochem 33:651–657 doi:10.1016/S0038-0717(00)00209-1

Pages L, Pellerin S (1996) Study of differences between vertical root maps observed in a maize crop and simulated maps obtained using a model for the three-dimensional architecture of the root system. Plant Soil 182:329–337

Patel DD, Barlow PW, Lee RB (1990) Development of vacuolar volume in the root-tips of pea. Ann Bot (Lond) 65:159–169

Paterson E (2003) Importance of rhizodeposition in the coupling of plant and microbial productivity. Eur J Soil Sci 54:741–750 doi:10.1046/j.1351-0754.2003.0557.x

Paterson E, Sim A (1999) Rhizodeposition and C-partitioning of *Lolium perenne* in axenic culture affected by nitrogen supply and defoliation. Plant Soil 216:155–164 doi:10.1023/A:1004789407065

Paterson E, Thornton B, Sim A, Pratt S (2003) Effects of defoliation and atmospheric CO_2 depletion on nitrate acquisition, and exudation of organic compounds by roots of *Festuca rubra*. Plant Soil 250:293–305 doi:10.1023/A:1022819219947

Paterson E, Thornton B, Midwood AJ, Sim A (2005) Defoliation alters the relative contributions of recent and non-recent assimilate to root exudation from *Festuca rubra*. Plant Cell Environ 28:1525–1533 doi:10.1111/j.1365-3040.2005.01389.x

Paterson E, Sim A, Standing D, Dorward M, McDonald AJS (2006) Root exudation from *Hordeum vulgare* in response to localized nitrate supply. J Exp Bot 57:2413–2420 doi:10.1093/jxb/erj214

Paterson E, Gebbing T, Abel C, Sim A, Telfer G (2007) Rhizodeposition shapes rhizosphere microbial community structure in organic soil. New Phytol 173:600–610 doi:10.1111/j.1469-8137.2006.01931.x

Paterson E, Osler G, Dawson LA, Gebbing T, Sim A, Ord B (2008) Labile and recalcitrant plant fractions are utilised by distinct microbial communities in soil: independent of the presence of roots and mycorrhizal fungi. Soil Biol Biochem 40:1103–1113 doi:10.1016/j.soilbio.2007.12.003

Patrick JW (1997) Phloem unloading: sieve element unloading and post-sieve element transport Ann Rev Plant Physiol. Plant Mol Biol 48:191–222 doi:10.1146/annurev.arplant.48.1.191

Paull RE, Jones RL (1975a) Studies on the secretion of maize root cap slime. 2. Localization of slime production. Plant Physiol 56:307–312 doi:10.1104/pp.56.2.307

Paull RE, Jones RL (1975b) Studies on the secretion of maize root-cap slime. 3. Histochemical and autoradiographic localization of incorporated fucose. Planta 127:97–110 doi:10.1007/BF00388371

Paull RE, Jones RL (1976a) Studies on the secretion of maize root cap slime. 4. Evidence for the involvement of dictyosomes. Plant Physiol 57:249–256 doi:10.1104/pp.57.2.249

Paull RE, Jones RL (1976b) Studies on the secretion of maize root cap slime. 5. The cell wall as a barrier to secretion. Zeit Pflanzenphysiol 79:154–164

Paull RE, Johnson CM, Jones RL (1975) Studies on the secretion of maize root cap slime. 1. Some properties of the secreted polymer. Plant Physiol 56:300–306 doi:10.1104/pp.56.2.300

Personeni E, Nguyen C, Marchal P, Pagès L (2007) Experimental evaluation of an efflux–influx model of C exudation by individual apical root segments. J Exp Bot 58:2091–2099 doi:10.1093/jxb/erm065

Pfeffer PE, Douds DD, Bücking H, Schwartz DP, Shachar-Hill Y (2004) The fungus does not transfer carbon to or between roots in an arbuscular mycorrhizal symbiosis. New Phytol 163:617–627

Philips DA, Fox TC, Six J (2006) Root exudation (net efflux of amino acids) may increase rhizodeposition under elevated CO_2. Glob Change Biol 12:561–567 doi:10.1111/j.1365-2486.2006.01100.x

Phillips RP, Fahey TJ (2005) Patterns of rhizosphere carbon flux in sugar maple (*Acer saccharum*) and yellow birch (*Betula allegheniensis*) saplings. Glob Change Biol 11:983–995 doi:10.1111/j.1365-2486.2005.00959.x

Phillips DA, Fox TC, King MD, Bhuvaneswari TV, Teuber LR (2004) Microbial products trigger amino acid exudation from plant roots. Plant Physiol 136:2887–2894 doi:10.1104/pp.104.044222

Pinton R, Varanini Z, Nannipieri P (2001) The rhizosphere. Biochemistry and organic substances at the soil–plant interface. CRC, Boca Raton

Qian JH, Doran JW, Walters DT (1997) Maize plant contributions to root zone available carbon and microbial transformations of nitrogen. Soil Biol Biochem 29:1451–1462 doi:10.1016/S0038-0717(97)00043-6

Quadt-Hallmann A, Hallmann J, Kloepper JW (1997) Bacterial endophytes in cotton: location and interaction with other plant associated bacteria. Can J Microbiol 43:254–259

Rangel-Castro JI, Killham K, Ostle N, Nicol GW, Anderson IC, Scrimgeour CM, Ineson P, Meharg A, Prosser JI (2005a) Stable isotope probing analysis of the influence of liming on root exudate utilization by soil microorganisms. Environ Microbiol 7:828–838 doi:10.1111/j.1462-2920.2005.00756.x

Rangel-Castro JI, Prosser JI, Ostle N, Scrimgeour CM, Killham K, Meharg A (2005b) Flux and turnover of fixed carbon in soil microbial biomass of limed and unlimed plots of an upland grassland ecosystem. Environ Microbiol 7:544–552 doi:10.1111/j.1462-2920.2005.00722.x

Read DB, Gregory PJ (1997) Surface tension and viscosity of axenic maize and lupin root mucilages. New Phytol 137:623–628 doi:10.1046/j.1469-8137.1997.00859.x

Read DJ, Perez-Moreno J (2003) Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? New Phytol 157:475–492 doi:10.1046/j.1469-8137.2003.00704.x

Read DB, Bengough AG, Gregory PJ, Crawford JW, Robinson D, Scrimgeour CM, Young IM, Zhang K, Zhang X (2003) Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. New Phytol 157:315–326 doi:10.1046/j.1469-8137.2003.00665.x

Roberts SK (2006) Plasma membrane anion channels in higher plants and their putative functions in roots. New Phytol 169:647–666 doi:10.1111/j.1469-8137.2006.01639.x

Robinson D, Fitter AH (1999) The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. J Exp Bot 50:9–13 doi:10.1093/jexbot/50.330.9

Rochette P, Flanagan LB, Gregorich EG (1999) Separating soil respiration into plant and soil components using analyses of the natural abundance of ^{13}C. Soil Sci Soc Am J 63:1207–1213

Rodger S, Bengough AG, Griffiths BS, Stubbs V, Young IM (2003) Does the presence of detached root border cells of *Zea mays* alter the activity of the pathogenic nematode *Meloidogyne incognita?*. Phytopath 93:1111–1114 doi:10.1094/PHYTO.2003.93.9.1111

Roose T, Fowler AC (2004) A mathematical model for water and nutrient uptake by plant root systems. J Theor Biol 228:173–184 doi:10.1016/j.jtbi.2003.12.013

Rosling A, Lindahl BD, Finlay RD (2004a) Carbon allocation in intact mycorrhizal systems of *Pinus sylvestris* L. seedlings colonizing different mineral substrates. New Phytol 162:795–802 doi:10.1111/j.1469-8137.2004.01080.x

Rosling A, Lindahl BD, Taylor AFS, Finlay RD (2004b) Mycelial growth and substrate acidification of ectomycorrhizal fungi in response to different minerals. FEMS Microbiol Ecol 47:31–37 doi:10.1016/S0168-6496(03)00222-8

Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. Can J Res 31:1855–1870 doi:10.1139/cjfr-31-11-1855

Roux SJ, Steinebrunner I (2007) Extracellular ATP: an unexpected role as a signaller in plants. Trends Plant Sci 11:522–527 doi:10.1016/j.tplants.2007.09.003

Rovira AD (1965) Interactions between plant roots and soil microorganisms. Annu Rev Microbiol 19:241–266 doi:10.1146/annurev.mi.19.100165.001325

Rovira AD (1969) Plant root exudates. Bot Rev 35:35–59 doi:10.1007/BF02859887

Rovira AD, Foster RC, Martin JK (1979) Note on terminology: origin, nature and nomenclature of the organic materials in the rhizosphere. In: Harley JL, Scott Russell R (eds) The soil–root interface. Academic, London, pp 1–4

Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. Ann Rev Plant Physiol Plant Mol Biol 52:527–560

Sacchi GA, 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 Soil 220:1–11 doi:10.1023/A:1004701912815

Samaj J, Read ND, Volkmann D, Menzel D, Baluska F (2005) The endocytic network in plants. Trends Cell Biol 15:425–433 doi:10.1016/j.tcb.2005.06.006

Samuels AL, Fernando M, Glass ADM (1992) Immunofluorescent localization of plasma-membrane H^+-ATPase in barley roots and effects of K-nutrition. Plant Physiol 99:1509–1514 doi:10.1104/pp.99.4.1509

Sapronov DV, Kuzyakov YV (2007) Separation of root and microbial respiration: comparison of three methods. Eurasian Soil Sci 40:775–784 doi:10.1134/S1064229307070101

Scheunert I, Topp E, Attar A, Korte F (1994) Uptake pathways of chlorobenzenes in plants and their correlation with n-octanol/water partition-coefficients. Ecotoxicol Environ Saf 27:90–104 doi:10.1006/eesa.1994.1009

Scheurwater I, Clarkson DT, Purves JV, van Rijt G, Saker LR, Welschen R, Lambers H (1999) Relatively large nitrate efflux can account for the high specific respiratory costs for nitrate transport in slow-growing grass species. Plant Soil 215:123–134 doi:10.1023/A:1004559628401

Schnepf A, Roose T (2006) Modelling the contribution of arbuscular mycorrhizal fungi to plant phosphate uptake. New Phytol 171:669–682

Schraut D, Ullrich CI, Hartung W (2004) Lateral ABA transport in maize roots (*Zea mays*): visualization by immunolocalization. J Exp Bot 55:1635–1641 doi:10.1093/jxb/erh193

Sherson SM, Alford HL, Forbes SM, Wallace G, Smith SM (2003) Roles of cell-wall invertases and monosaccharide transporters in the growth and development of Arabidopsis. J Exp Bot 54:525–531 doi:10.1093/jxb/erg055

Shishkova S, Dubrovsky JG (2005) Developmental programmed cell death in primary roots of Sonoran Desert Cactaceae. Am J Bot 92:1590–1594 doi:10.3732/ajb.92.9.1590

Shrestha M, Abraham WR, Shrestha PM, Noll M, Conrad R (2008) Activity and composition of methanotrophic bacterial communities in planted rice soil studied by flux measurements, analyses of pmoA gene and stable isotope probing of phospholipid fatty acids. Environ Microbiol 10:400–412 doi:10.1111/j.1462-2920.2007.01462.x

Simard SW, Perry DA, Jones MD, Myrold DD, Durall DM, Molina R (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388:579–582 doi:10.1038/41557

Singh BK, Millard P, Whiteley AS, Murrell JC (2004) Unravelling rhizosphere–microbial interactions: opportunities and limitations. Trends Microbiol 12:386–393 doi:10.1016/j.tim.2004.06.008

Singh BK, Naoise N, Ridgway KP, McNicol J, Young JPW, Daniell TJ, Prosser JI, Millard P (2008) Relationship between assemblages of mycorrhizal fungi and bacteria on grass roots. Environ Microbiol 10:534–541 doi:10.1111/j.1462-2920.2007.01474.x

Sobolev VS, Potter TL, Horn BW (2006) Prenylated stilbenes from peanut root mucilage. Phytochem Anal 17:312–322 doi:10.1002/pca.920

Srivastava S, Srivastava AK (2007) Hairy root culture for mass-production of high-value secondary metabolites. Crit Rev Biotechnol 27:29–43 doi:10.1080/07388550601173918

Staddon PL, Bronk Ramsey C, Ostle N, Ineson P, Fitter AH (2003) Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of ^{14}C. Science 300:1138–1140 doi:10.1126/science.1084269

Stewart AM, Frank DA (2008) Short sampling intervals reveal very rapid root turnover in a temperate grassland. Oecologia 157:453–458 doi:10.1007/s00442-008-1088-9

Stubbs VEC, Standing D, Knox OGG, Killham K, Bengough AG, Griffiths B (2004) Root border cells take up and release glucose-C. Ann Bot (Lond) 93:221–224 doi:10.1093/aob/mch019

Sugiyama A, Shitan N, Yazaki K (2007) Involvement of a soybean ATP-binding cassette—type transporter in the secretion of genistein, a signal flavonoid in legume–rhizobium symbiosis. Plant Physiol 144:2000–2008 doi:10.1104/pp.107.096727

Sun Y-P, Unestam T, Lucas SD, Johanson KJ, Kenne L, Finlay RD (1999) Exudation–reabsorption in mycorrhizal fungi, the dynamic interface for interaction with soil and other microorganisms. Mycorrhiza 9:137–144 doi:10.1007/s005720050298

Swinnen J (1994) Rhizodeposition and turnover of root-derived organic material in barley and wheat under conventional and integrated management. Agric Ecosyst Environ 51:115–128 doi:10.1016/0167-8809(94)90038-8

Swinnen J, van Veen JA, Merckx R (1995) Root decay and turnover of rhizodeposits in field-grown winter-wheat and spring barley estimated by ^{14}C pulse-labeling. Soil Biol Biochem 27:211–217 doi:10.1016/0038-0717(94)00161-S

Thaler P, Pages L (1998) Modelling the influence of assimilate availability on root growth and architecture. Plant Soil 201:307–320 doi:10.1023/A:1004380021699

Thornton B (2001) Uptake of glycine by non-mycorrhizal *Lolium perenne*. J Exp Bot 52:1315–1322 doi:10.1093/jexbot/52.359.1315

Thornton B, Paterson E, Midwood AJ, Sim A, Pratt SM (2004) Contribution of current carbon assimilation in supplying root exudates of *Lolium perenne* measured using steady-state ^{13}C labelling. Physiol Plant 120:434–441 doi:10.1111/j.0031-9317.2004.00250.x

Todorovic C, Nguyen C, Robin C, Guckert A (2001) Root and microbial involvement in the kinetics of C-14-partitioning to rhizosphere respiration after a pulse labelling of maize assimilates. Plant Soil 228:179–189 doi:10.1023/A:1004830011382

Toljander JF, Artursson V, Paul LR, Jansson JK, Finlay RD (2006) Attachment of different soil bacteria to arbuscular mycorrhizal fungi is determined by hyphal vitality and fungal species. FEMS Microbiol Lett 254:34–40 doi:10.1111/j.1574-6968.2005.00003.x

Toljander JF, Paul L, Lindahl BD, Elfstrand M, Finlay RD (2007) Influence of AM fungal exudates on bacterial community structure. FEMS Microbiol Ecol 61:295–304 doi:10.1111/j.1574-6941.2007.00337.x

Treseder KK, Turner KM (2007) Glomalin in ecosystems. Soil Sci Soc Am J 71:1257–1266 doi:10.2136/sssaj2006.0377

van Hees PAW, Jones DL, Finlay R, Godbold DL, Lundström U (2005) The carbon we do not see—the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review. Soil Biol Biochem 37:1–13 doi:10.1016/j.soilbio.2004.06.010

Vandenkoornhuyse P, Mahé S, Ineson P, Staddon P, Ostle N, Cliquet J-B, Francez A-J, Fitter AH, Young JPW (2007) Active root-inhabiting microbes identified by rapid incorporation of plant-derived carbon into RNA. Proc Natl Acad Sci U S A 104:16970–16975 doi:10.1073/pnas.0705902104

Verpoorte R, van der Heijden R, Memelink J (2000) Engineering the plant cell factory for secondary metabolite production. Transgenic Res 9:323–343 doi:10.1023/A:1008966404981

Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586 doi:10.1023/A:1026037216893

Wallander H, Nilsson LO, Hagerberg D, Bååth E (2001) Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. New Phytol 151:752–760 doi:10.1046/j.0028-646x.2001.00199.x

Warembourg FR, Kummerow J (1991) Photosynthesis/translocation studies in terrestrial ecosystems. In: Coleman DC, Fry B (eds) Carbon isotope techniques. Academic, London, pp 11–37

Watt M, Hugenholtz P, White R, Vinall K (2006) Numbers and locations of native bacteria on field-grown wheat roots quantified by fluorescence in situ hybridization (Fish). Environ Microbiol 8:871–884 doi:10.1111/j.1462-2920.2005.00973.x

Welbaum GE, Sturz AV, Dong ZM, Nowak J (2007) Managing soil microorganisms to improve productivity of agro-ecosystems. Crit Rev Plant Sci 23:175–193 doi:10.1080/07352680490433295

Wen FS, VanEtten HD, Tsaprailis G, Hawes MC (2007) Extracellular proteins in pea root tip and border cell exudates. Plant Physiol 143:773–783 doi:10.1104/pp.106.091637

Whipps JM (2001) Microbial interactions and biocontrol in the rhizosphere. J Exp Bot 52:487–511

Wichern F, Mayer J, Joergensen RG, Muller T (2007) Rhizodeposition of C and N in peas and oats after ^{13}C-^{15}N double labelling under field conditions. Soil Biol Biochem 39:2527–2537 doi:10.1016/j.soilbio.2007.04.022

Williams LE, Lemoine R, Sauer N (2000) Sugar transporters in higher plants—a diversity of roles and complex regulation. Trends Plant Sci 5:283–290 doi:10.1016/S1360-1385(00)01681-2

Wright DP, Read DJ, Scholes JD (1998) Mycorrhizal sink strength influences whole plant carbon balance of *Trifoli-*

um repens L. Plant Cell Environ 21:881–891 doi:10.1046/j.1365–3040.1998.00351.x

Wuyts N, Maung ZTZ, Swennen R, De Waele D (2006) Banana rhizodeposition: characterization of root border cell production and effects on chemotaxis and motility of the parasitic nematode *Radopholus similis*. Plant Soil 283:217–228 doi:10.1007/s11104-006-0013-4

Yeomans CV, Porteous F, Paterson E, Meharg AA, Killham K (1999) Assessment of lux-marked *Pseudomonas fluorescens* for reporting on organic carbon compounds. FEMS Microbiol Lett 176:79–83 doi:10.1111/j.1574-6968.1999.tb13645.x

Zhang WH, Ryan PR, Tyerman SD (2004) Citrate-permeable channels in the plasma membrane of cluster roots from white lupin. Plant Physiol 136:3771–3783 doi:10.1104/pp.104.046201

Zhao XW, Schmitt M, Hawes MC (2000) Species-dependent effects of border cell and root tip exudates on nematode behaviour. Phytopath 90:1239–1245 doi:10.1094/PHYTO.2000.90.11.1239

Zheng J, Sutton JC, Yu H (2000) Interactions among *Pythium aphanidermatum*, roots, root mucilage, and microbial agents in hydroponic cucumbers. Can J Plant Pathol 22:368–379

Zhu T, Rost TL (2000) Directional cell-to-cell communication in the Arabidopsis root apical meristem. III. Plasmodesmata turnover and apoptosis in meristem and root cap cells during four weeks after germination. Protoplasma 213:99–107 doi:10.1007/BF01280510