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

D. L. Jones · C. Nguyen · R. D. Finlay

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.

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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
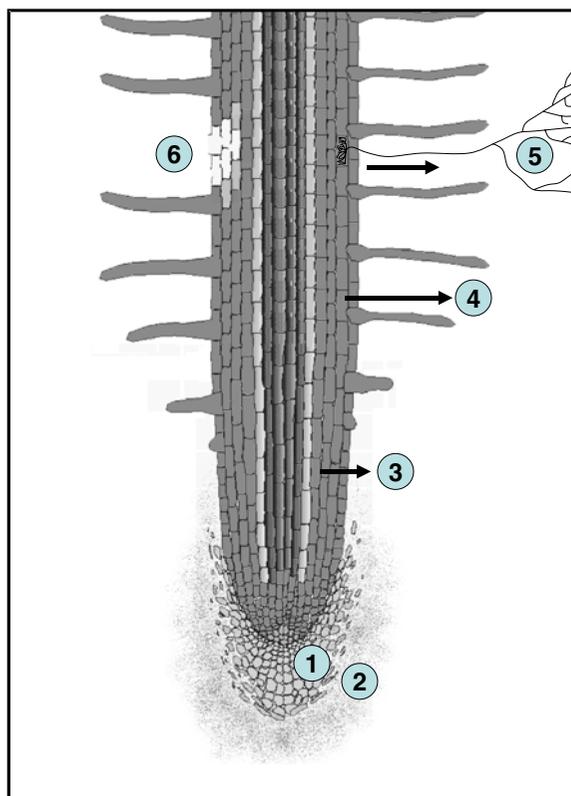

Fig. 1 Schematic representation of a longitudinal section of a growing root showing the six major sites of rhizodeposition: *1* loss of root cap and border cells, *2* loss of insoluble mucilage, *3* loss of soluble root exudates, *4* loss of volatile organic C, *5* loss of C to symbionts (e.g. arbuscular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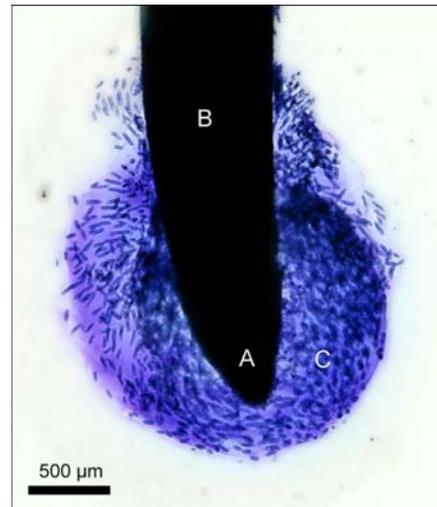

Fig. 2 Light microscope image showing the large amount of mucilage (blue halo surrounding the root) and border cells production in a Zea mays L. root tip. Labels indicate the root quiescent centre (A), the main root elongation zone (B), and the mucilage halo in which the border cell are embedded (C). 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; C– 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
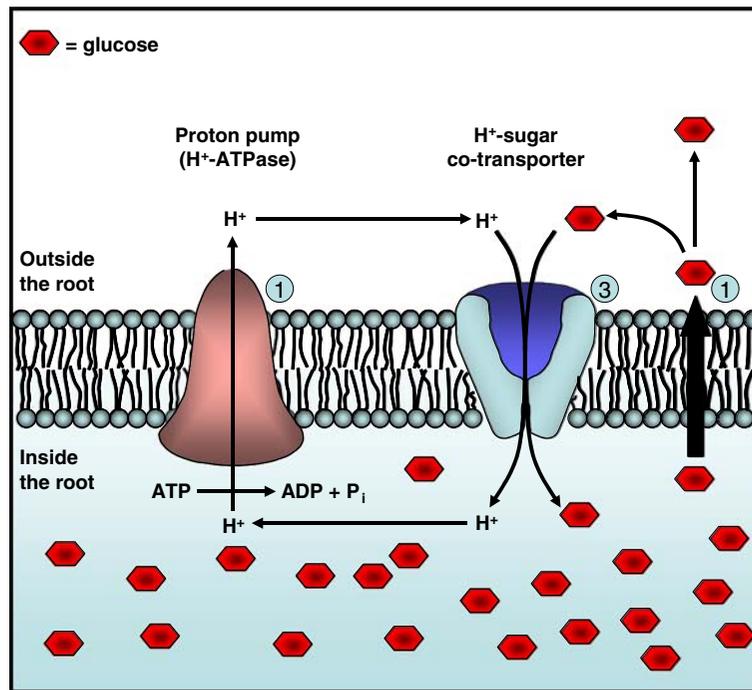
Fig. 3 Schematic representation of the three main processes involved in the bi-directional flux of low molecular weight organic solutes (e.g. glucose) across the soil root interface. Flux (*1*) denotes the passive transport of glucose across the plasma membrane in response to the large cytoplasm (20 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 (Verporte 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
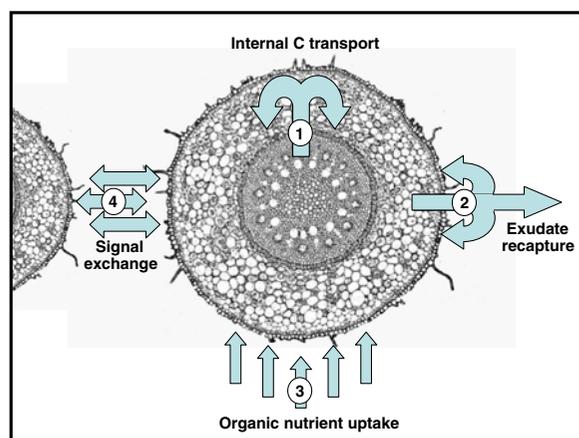

Fig. 4 Schematic representation of a transverse root section illustrating the four principal hypotheses explaining the uptake of organic C from soil: *1* indirect, fortuitous root exudate recapture in the root's internal apoplastic transport and signalling pathways, *2* direct recapture of root exudates 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

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).

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. δ^{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 photoassimilates (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
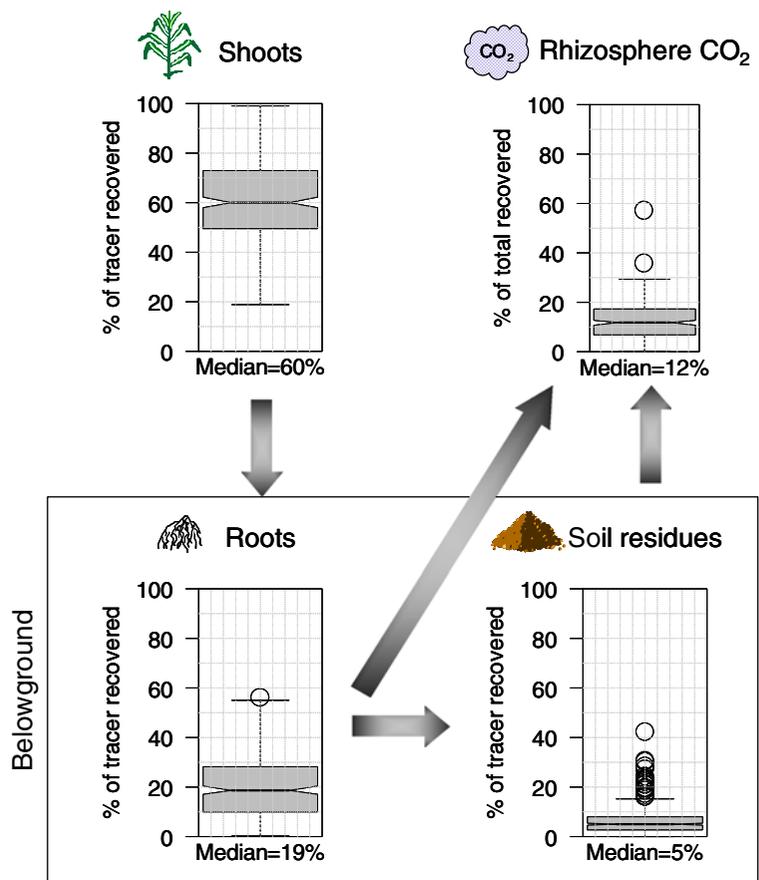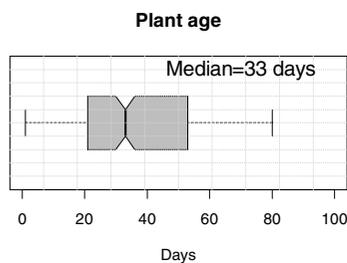
Fig. 5 Partitioning of labeled net fixed C after a pulse or continuous exposure of shoots to a $^{14}CO_2$ enriched atmosphere. For each compartment, *boxplots* show the distribution of 271 individual partition coefficients drawn from a review of the literature by Nguyen (2003) and updated to 2007. The 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
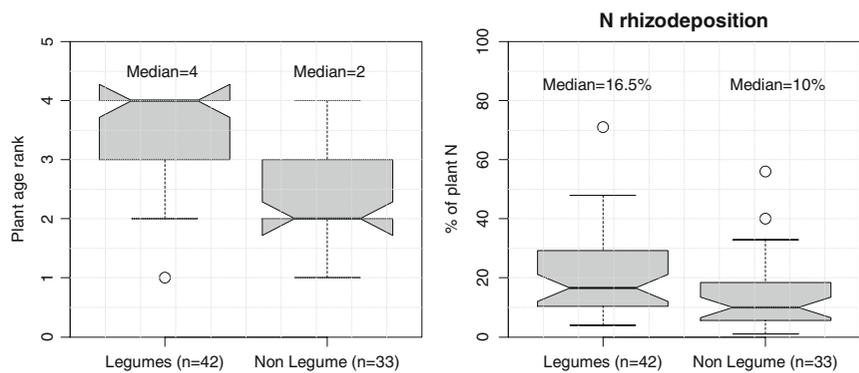
Fig. 6 Summary of published studies on N rhizodeposition expressed as a percentage of total plant N. Rhizosphere N derived from roots was determined by labeling of plant N with ^{15}N supplied as $^{15}NH_3$, $^{15}NO_3$ or ^{15}N-urea. The technique used was one of the following: split-root cultures, 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)
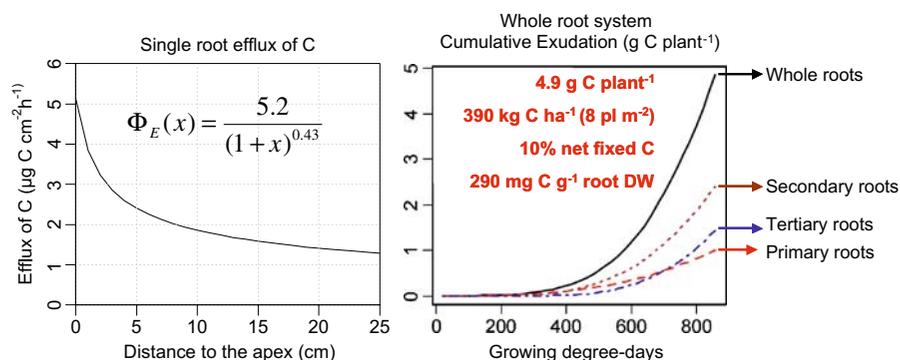

Fig. 7 Modelling of root exudation in maize. *Left*: Experimentally parameterized efflux profile of C from a single root (from Personeni et al. 2007). *Right*: Mathematical simulation of whole root system exudation in maize from germination until flowering (860 growing degree days, base 6°C). The simulation 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 land-scape 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 hydro-logically 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.

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