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Review

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Plant and mycorrhizal regulation of rhizodeposition

Author for correspondence:
David L. Jones
Tel: +44 1248382579
Fax: +44 1248354997
Email: d.jones@bangor.ac.uk

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David L. Jones[1], Angela Hodge[2] and Yakov Kuzyakov[3]

[1]School of Agricultural and Forest Sciences, University of Wales, Bangor, Gwynedd, LL57 2UW, Wales, UK; [2]Department of Biology, University of York, PO Box 373, York YO10 5YW, England, UK; [3]Department of Soil Science and Land Evaluation, Institute of Soil Science and Land Evaluation, Hohenheim University, Emil-Wolff-Strasse 27, D-70599 Stuttgart

Contents

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Summary

The loss of carbon from roots (rhizodeposition) and the consequent proliferation of microorganisms in the surrounding soil, coupled with the physical presence of a root and processes associated with nutrient uptake, gives rise to a unique zone of soil called the rhizosphere. In this review, we bring together evidence to show that roots can directly regulate most aspects of rhizosphere C flow either by regulating the exudation process itself or by directly regulating the recapture of exudates from soil. Root exudates have been hypothesized to be involved in the enhanced mobilization and acquisition of many nutrients from soil or the external detoxification of metals. With few exceptions, there is little mechanistic evidence from soil-based systems to support these propositions. We conclude that much more integrated work in realistic systems is required to quantify the functional significance of these processes in the field. We need to further unravel the complexities of the rhizosphere in order to fully engage with key scientific ideas such as the development of sustainable agricultural systems and the response of ecosystems to climate change.

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I. Introduction

A mechanistic understanding of carbon (C) dynamics in terrestrial ecosystems is a prerequisite to the advancement of a number of scientific areas including the development of sustainable agricultural systems and the prediction of ecosystem responses to anthropogenic pollution and climate change (Paterson *et al.*, 1997; Cheng & Johnson, 1998). While the total amount of C contained within a terrestrial ecosystem is relatively easy to calculate, and the rate of C entry into the plant and out of the soil is relatively easy to measure, the below ground exchange of C between the plant and soil pool remains poorly understood. This uncertainty is caused by the complex nature of soil foodwebs, the interactions of plant and soil C flow and the imposition of external factors upon these (e.g. land management, climate; van de Geijn & van Veen, 1993, Fig. 1). In addition, our lack of fundamental understanding of below-ground C flow often comes from a lack of appreciation of this intrinsic complexity and the lack of suitable techniques capable of addressing it (Swinnen *et al.*, 1994; Kuzyakov, 2001). Consequently, mechanistic rhizosphere C flow research has almost entirely been undertaken in the laboratory in microcosms, often in the absence of soil. The aim of this review is firstly to examine the factors that regulate root C flow, including the impact of mycorrhizas and other factors, and secondly to examine the functional significance of certain aspects of rhizosphere C flow from an ecological perspective (e.g. nutrient cycling). We do not aim to produce a definitive literature review on all aspects of rhizosphere C flow but to challenge current assumptions and, where possible, to identify knowledge gaps and possible solutions. It must be noted that our understanding of the mechanistic processes involved in rhizodeposition is highly fragmented. Further, research in this area has tended to focus on monocotyledonous crop plants. It is known that rhizodeposition patterns can vary widely both within and between plant species (Ryan *et al.*, 1995; Van der Krift *et al.*, 2001; Fig. 1), however, it is our intention here to focus on uniform patterns of response.

II. What is rhizodeposition?

The release of carbon compounds from living plant roots (rhizodeposition) into the surrounding soil is a ubiquitous phenomenon (Curl & Trueglove, 1986). The loss of C from root epidermal and cortical cells leads to a proliferation of microorganisms within (endorhizosphere), on the surface (rhizoplane) and outside the root (ectorhizosphere; Lynch & Whipps, 1990). C release also results in the rhizosphere having different chemical, physical and biological characteristics to the bulk soil (Barber, 1995). The magnitude of these changes in soil properties is largely determined by the amount and type of C released from the root, as well as intrinsic soil characteristics (Fig. 1; Kuzyakov & Domanski, 2000; Tinker & Nye, 2000). Theoretically, almost any soluble component present inside the root can be lost to the rhizosphere; however, current evidence suggests that exudation is dominated by low molecular weight solutes such as sugars, amino acids and organic acids that are present in the cytoplasm at high concentrations (Farrar *et al.*, 2003). Despite hundreds of reports of root exudation there are few reliable quantitative estimates of the flux of individual solutes from the cytoplasm into the soil or the mechanistic basis of their release (Uren, 2001; Farrar *et al.*, 2003). Consequently, without a fundamental knowledge of how root exudation is regulated it is impossible to understand its ecological significance.

III. Regulation of rhizodeposition

The continual release of carbon compounds from the root into the soil falls into two classes: exudates which are lost simply as a result of passive diffusion and over which the plant exerts little control (basal exudation); and exudates which are released for a specific purpose and over which the plant exerts a close degree of control. In the second category, diffusion may still be the primary mechanism of exudate release, however, the opening of membrane pores (e.g. anion channels) may increase the effective diffusion rate by several orders of magnitude (Jones, 1998). The net rate of loss of individual charged compounds in basal exudation can be described by the net flux density equation

$$J = P(1/(e^{zFEm/RT} - 1))(C_o - (C_i e^{zFEm/RT})) \quad \text{Eqn 1}$$

where the flux (J) is controlled by the charge of the solute (z), the membrane permeability coefficient of the solute (P), the concentration in the cytoplasm (C_i) and in the soil (C_o), the plasma membrane potential (Em) and temperature (T) with F being the Faraday constant (Nobel, 1983). After the cancellation of the charged terms, the equation for uncharged solutes becomes

$$J = P(C_o - C_i) \quad \text{Eqn 2}$$

Despite the relative simplicity of these equations, few researchers have used them to predict exudation rates. Measured exudation rates in maize roots are in fact similar to those predicted with the net flux density equation suggesting that basal exudation is diffusion mediated (Jones & Darrah, 1996). There are, however, some difficulties associated with the parameterization of these equations, including the difficulty in measuring cytoplasmic solute concentrations (C_i), the amount of root surface area contributing to exudation and the limited data available on root membrane permeability coefficients (P). In most cases, the concentration gradient across the plasma membrane is very large, with solutes in the cytoplasm being in the concentration range of 0.5–10 mM while corresponding concentrations in the soil are very much lower (0.1–50 μM; Jones *et al.*, 1996, 2003). We hypothesize that this large gradient is continually maintained as a result of the constant removal

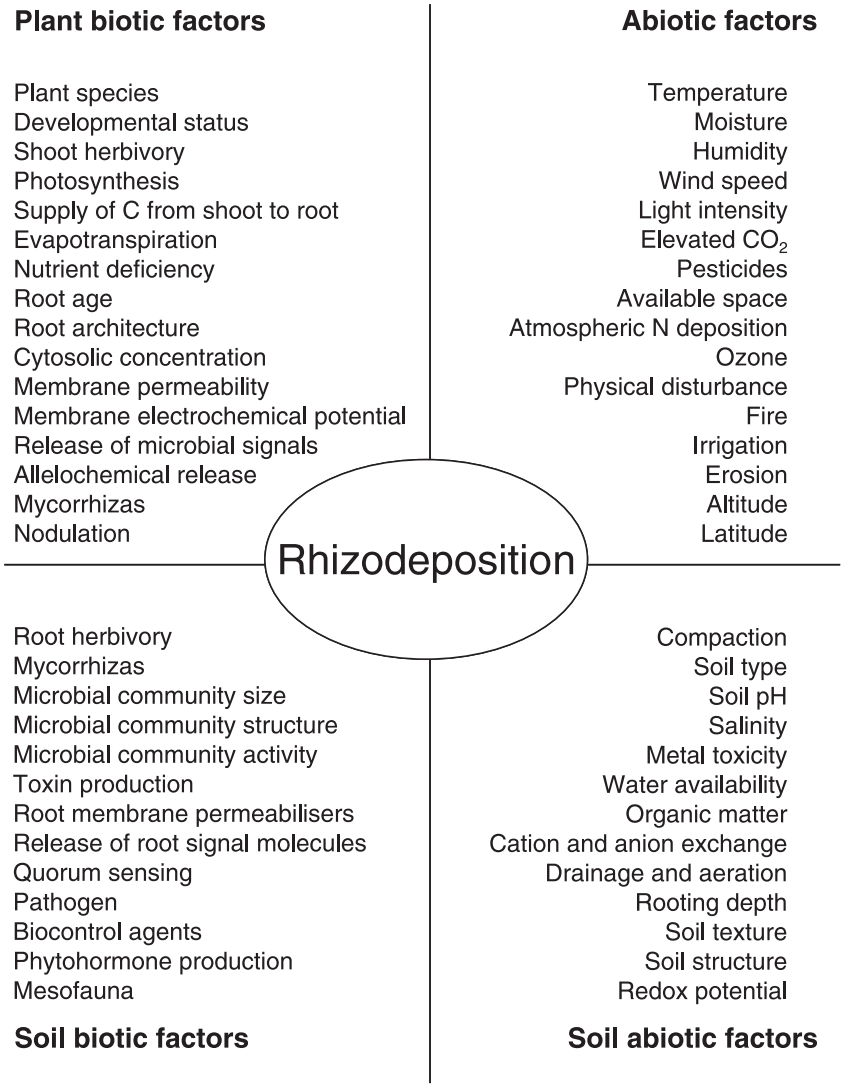

Fig. 1 Schematic representation of the biotic and abiotic factors of plant and soil that influence rhizodeposition.

of exudates from the soil solution by either biotic (e.g. soil microbial uptake; Kuzyakov *et al.*, 2003) or abiotic processes (e.g. sorption; van Hees *et al.*, 2002, 2003). In the case of uncharged solutes such as sugars, it is likely that loss from roots occurs simply as a result of passive diffusion down the large concentration gradient (Eqn 1). Current evidence suggests that sugars such as glucose dominate root exudates (Jones & Darrah, 1996; Lugtenberg *et al.*, 1999; Toal *et al.*, 2000). By contrast, high molecular weight solutes such as proteins are largely prevented from diffusing across the plasma membrane into the soil by their low membrane permeability coefficients and their inability to pass through the small apertures in the cell wall (Fry, 1988). It is theoretically possible that basal exudation could be regulated in root cells by altering either the size of the diffusion gradient, membrane potential, or the permeability of the membrane (e.g. by altering membrane lipid and protein composition; Eqn 1). However, we hypothesize that after millions of years of plant evolution, membranes are highly optimized and that further regulation would be difficult without compromising other aspects of cellular function (e.g. cell signalling, cytoskeletal regulation, nutrient uptake, etc.; Arango *et al.*, 2003). Based upon a range of studies, it is likely that basal root exudation constitutes approx. 3–5% of C fixed in photosynthesis (Pinton *et al.*, 2001). However, under a range of biotic and abiotic stresses (e.g. nutrient deficiency, hypoxia, pathogen attack, drought), the rate of exudation can increase significantly as a result of loss of membrane integrity or a breakdown in normal cell metabolism (Neumann & Römheld, 2001). In many circumstances, plants appear to exert little control over their C loss (e.g. during drought stress) and the compounds lost appear to have little functional roles in alleviating stress (e.g. enhanced sugar exudation under Ca^{2+} deficiency; Uren, 2001). We hypothesize therefore that many plants may exert little direct control over large components of their C efflux. However, under a variety of biotic and abiotic stress conditions, there is evidence to suggest that while C efflux

cannot be down-regulated it can be directly up-regulated to help alleviate stress (Jones, 1998). Examples of this include the exudation of organic acids by wheat roots which prevent rhizotoxic Al entering the root (Ryan *et al.*, 1995), the dumping in the soil of metabolites generated during anaerobic respiration in maize roots (Xia & Saglio, 1992) and the release of organic acids under P deficiency (Lambers *et al.*, 2002).

In our opinion we consider that the build up of C compounds in the rhizosphere would not a desirable plant trait, as microbial proliferation in response to this labile C may enhance competition for nutrients and also increase the likelihood of pathogen attraction, growth and attack (Liu *et al.*, 1997; Nguyen, 2003). Exceptions to this would occur when exudates are released to overcome stress related events where a direct positive benefit to the plant occurs (Wu *et al.*, 1999; Pineros *et al.*, 2002; Veneklaas *et al.*, 2003). Evidence suggests that roots may employ a range of strategies to minimize the negative effects of C loss. Recently it has been proposed that border cells may act as a temporary decoy drawing pathogenic organisms away from the root (Gunawardena & Hawes, 2002; Rodger *et al.*, 2003). Alternatively, roots could release antimicrobial compounds, although there is little evidence to support this as a universal mechanism (Schenk *et al.*, 1991). Unfortunately, the effect of an ectomycorrhizal sheath around the root on exudation remains unknown, however, it may be expected that the presence of the fungus would significantly reduce the amount and rate of diffusion of exudates into the soil. Plants can also retrieve C lost into the soil (Sacchi *et al.*, 2000; Owen & Jones, 2001; Persson & Nasholm, 2003).

Carbon flow in the rhizosphere is often assumed to be a unidirectional flux whereby C moves out of roots into the surrounding soil (Marschner, 1995). There is now a significant body of evidence to suggest that a number of exudate components can be actively taken back into the root (Jones & Darrah, 1993; Muhling *et al.*, 1993). This re-absorption of C largely applies to those compounds lost in greatest quantities from roots (i.e. sugars and amino acids). However, roots can also take up a variety of compounds which do not represent major components of root exudate and for which a functional role remains unclear (e.g. polyamines such as putrescine; Hart *et al.*, 1992; Kuiper *et al.*, 2001). It has been shown that the influx and efflux of C compounds at the soil–root interface occurs simultaneously, and that unlike the efflux component, the influx component is under direct plant control (Farrar *et al.*, 2003). This finding represents a major problem in rhizosphere research, in that almost all previous studies have not considered this influx component. Most experiments quantifying C exudation have used sterile, hydroponic cultures where exudates are typically collected over a period of days or weeks (Neumann & Römheld, 2001). Under these conditions, where the microbial sink has been removed, sugars and amino acids are simply lost and then reabsorbed (Jones *et al.*, 1996). As a result, only a small accumulation is observed in the external medium representing the equilibrium between passive efflux and active influx (Kraffczyk *et al.*, 1984). Indeed, if the external medium is supplemented with high concentrations of sugars and amino acids these are rapidly depleted by cereal roots until the influx-efflux equilibrium is again reached (Jones & Darrah, 1994). Consequently, the actual rate of C efflux from roots is likely to have been vastly underestimated, and most previous research can be viewed as being qualitative rather than quantitative. The re-uptake of sugars and amino acids by roots is mediated by a range of H^+-ATPase activated, solute-specific, plasma membrane H^+-cotransport systems (Rausch, 1991). While these transporters have been intensively studied at a molecular and physiological level, the ecological significance of these transporters has received little interest (Sakr *et al.*, 1997; Rentsch *et al.*, 1998; Wipf *et al.*, 2002). These inwardly directed transporters are also capable of capturing amino acids and sugars produced during the microbial breakdown of soil organic matter turnover (Chapin *et al.*, 1993). Based upon soil solution concentrations of mono- and disaccharides, the role of exogenous sugar uptake is likely to be of little ecological significance in photosynthetic plants. However, in the case of amino acids there has recently been intense speculation that capture of amino acids from soil organic matter may be a significant source of N (see below). There is also the possibility that these transport systems may be involved in signal exchange between soil microorganisms and roots although there is little direct evidence to support this (e.g. peptide uptake via peptide transporters; Williams & Miller, 2001).

From a limited range of studies in crop plants it appears that exudate recapture can occur along the whole length of the root and that the kinetics of the transporters are similar to those for inorganic nutrients (Jones & Darrah, 1994, 1996; Barber, 1995) and of the soil microorganisms with which they are presumably in competition (Jones & Hodge, 1999). Although there has been few studies on the regulation of root transporters involved in exudate recapture, in maize seedling roots the transport systems appear to be constitutively expressed and not down-regulated by the presence of inorganic N (Jones & Darrah, 1994; Bhattacharya *et al.*, 2002) while in Scots Pine, amino acid uptake is repressed by NH_4^+ (Persson & Nashölm, 2002). Conversely, in Arabidopsis inorganic N transporters are down-regulated by amino acids (Nazoa *et al.*, 2003). Although we have a basic understanding of how C loss from roots in some plant species may be regulated by influx, there is a need to confirm the significance of this exudate recapture phenomenon under a range of soil conditions and a need to understand how these transporters are regulated at a molecular and physiological level, firstly in hydroponics and then in soil.

Apart from sugars and amino acids, organic acids typically represent the next largest exudate group (Jones *et al.*, 2003). Because of the negative charge associated with organic acids in the cytoplasm (e.g. $succinate^{2-}$ and $citrate^{3-}$) their rate of exudation is enhanced by the electrochemical potential gradient across the membrane (Eqn 1; Jones, 1998). The rate of efflux

can be enhanced by an order of magnitude when organic acid-specific anion channels are open (Ryan *et al.*, 2001). By contrast to amino acids and sugars, however, there is little evidence that di- and trivalent organic acids can be taken back up into cereal roots either in the anionic (e.g. citrate^{3-}, malate^{2-}) or neutral state (e.g. H_3-citrate, Fe-citrate), although monovalent anions such as acetate can enter the root particularly in an undissociated state (Herrmann & Felle, 1995; Jones & Darrah, 1995). The reason for the lack of an uptake system for organic acids in roots is unknown, but we speculate that organic acids act in nutrient acquisition (see below) and consequently there is little benefit in recapture, particularly as the efflux rate is low in comparison to sugars and amino acids. Additionally, while amino acids and sugars are primarily used by the microbial community for growth, organic acids are used primarily for respiration and consequently may not induce microbial proliferation in the rhizosphere (Jones *et al.*, 2003).

IV. How large is the root exudation C flux?

Soil provides a formidable technical barrier to measuring the fluxes of individual C compounds or total C in the rhizosphere, and experimental approaches have relied on techniques which have been widely criticised (Meharg, 1994). In the first main approach, C partitioning in the plant and rhizosphere has been examined by destructive sampling, typically on sets of plants harvested at intervals of days or weeks. Whilst subsequent analyses of individual compounds may be fairly detailed, particularly if the plants are grown in hydroponic culture (Kraffczyk *et al.*, 1984), this approach provides only a snapshot of the outcome of many concurrent processes without providing an understanding of how those processes unfold in an individual plant and its rhizosphere (Dilkes *et al.*, 2004). Moreover, if the export of fixed carbon from leaves fluctuates over a timescale of minutes to hours (Farrar & Farrar, 1995), isolated or intermittent sampling times may not be appropriate for observing C fluxes to roots and rhizosphere. A second complementary and noninvasive approach is the collection of fractions of isotopically labelled CO_2 respired from the soil-root continuum as an estimate of the magnitude of below-ground processes (Högberg *et al.*, 2001). This can only provide a composite picture of root-plus-microbial respiration rather than differentiating between individual fluxes.

In a summary of 95 whole plant ^{14}C labelling studies performed in soil on a broad range of plant species, we estimated that approx. 5–10% of the net fixed C is lost by root exudation, while experiments performed in hydroponics show that typically only 0.5–1.5% of fixed C is lost (Farrar *et al.*, 2003). We ascribe this to a methodological bias causing underestimation of rhizosphere C flow in hydroponics (see above) and overestimation of rhizosphere C flow in soil (Meharg, 1994). It is likely that a true estimate of root exudation lies somewhere in between these values (i.e. a loss of 2–4% of net fixed C).

The amount of C entering the soil from plants (e.g. via root exudation, respiration or turnover) is important from a soil quality and climate change perspective. However, the rate of C loss to the soil by root exudation as opposed to root turnover has rarely been compared in the same experiment. This is largely because it is difficult operationally to divide exudation from living or senescing roots from C addition by dead or dying roots. The definition employed here is that exudation only occurs from metabolically active respiring roots while loss of soluble C from nonmetabolically active roots is termed lysis. From studies on excised root tips of maize it has been ascertained that roots can remain metabolically active for at least 48 h before their internal C reserves become exhausted by respiration (James *et al.*, 1993; Xia & Roberts, 1994; Chevalier *et al.*, 1995). One mechanism which is therefore vital in understanding C inputs into soil via roots is the mechanism by which roots die. We can differentiate between three states of root death: (1) nonapoptotic death where metabolic activity immediately ceases and all the C and nutrients from the roots enter the soil (e.g. when the root is mechanically damaged and mass lysis occurs) (2) nonapoptotic death where roots become excised, remain metabolically active and slowly deplete and exhaust internal soluble C reserves (e.g. severage of the main root axis by mesofauna), and (3) apoptotic death where re-translocation of both C and nutrients occurs to other growing areas of the plant (e.g. shutdown after exhaustion of a patch of soil; Gordon & Jackson, 2000). In each of these three scenarios the quantity, quality and lability of C inputs can be expected to be different. Further, the rate of exudation from roots in (2) and (3) remains unknown. It is clear therefore that whilst C flow from exudation is poorly understood, our knowledge of other key intertwined aspects of the below ground C cycle are similarly vague.

The key question which remains to be answered is the extent to which C flow varies spatially and temporally in the rhizosphere and how this is linked to microbial and root ecology? Although we have gained glimpses of this complexity (Fig. 2; Phillips *et al.*, 2003; Siegel *et al.*, 2003), to answer this will require a greater emphasis on *in vivo* studies performed in representative soil and climatic conditions tackled with a multidisciplinary approach (i.e. not just a cereal seedling in sterile hydroponic culture).

V. How responsive is the root exudation C flux?

In vegetative cereal and grass crops, photosynthetically fixed C is transported very rapidly below ground and can be detected in the environment external to the root in less than 1 h from photosynthetic fixation (Minchin *et al.*, 1994; Rattray *et al.*, 1995; Nguyen *et al.*, 1999; Kuzyakov & Cheng, 2001; Dilkes *et al.*, 2004). When exudation was quantified with fine temporal resolution, Dilkes *et al.* (2004) found that maximal exudation of recent photosynthate occurred within 3 h of fixation, with the exudation profile being sigmoidal in shape. The speed

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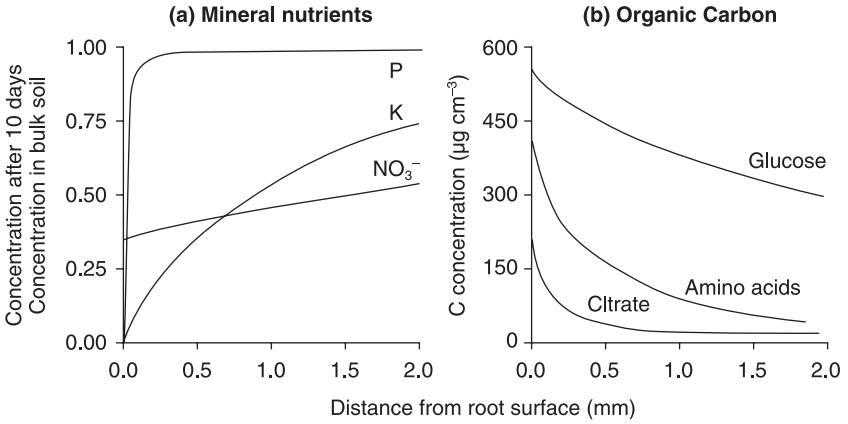

Fig. 2 Schematic representation of solute gradients in the rhizosphere illustrating that every position in the rhizosphere is chemically unique. (a) The depletion gradients of three inorganic solutes (N, P and K) in the rhizosphere caused by root uptake. (b) The accumulation gradients of three organic solutes (glucose, amino acids and citrate) in the rhizosphere caused by root exudation. Developed from Barber (1995), Tinker & Nye (2000), Jones *et al*. (1996) and Darrah (1991a,b,c).

with which recent photosynthate was lost to the rhizosphere indicates a very close link between current photosynthesis and exudation. However, Dilkes *et al.* (2004) found that exudation is more directly linked to the rate of carbon import into the root than to the rate of photosynthesis itself. It appears that the quantity exuded is closely coupled to root import of soluble sugars and, by inference, to the concentration of soluble sugars in the root (Dilkes *et al.*, 2004; Eqns 1 and 2).

Components of exudation are regulated over longer timescales in response to physiological changes and gene expression patterns at the whole plant level. For example, in many cases a period of days is required to induce enhanced exudation in response to mineral deficiency (e.g. phytosiderophore release under Fe deficiency; Ma *et al.*, 2003). In addition, shoot signals may be involved in triggering both exudation and the formation of root structures involved in exudation (Gilbert *et al.*, 2000; Li *et al.*, 2000; Shen *et al.*, 2003). The shoot may also play an indirect role in regulating exudation through the rate of sugar supply to the root as the concentration of free sugars in the root is a component of the signal transduction pathway involved in regulating root architecture and nutrient uptake (Bingham *et al.*, 1998; Freixes *et al.*, 2002; Lejay *et al.*, 2003).

VI. How responsive is the microbial community to root exudation?

Whole plant ^{14}C-labelling suggests that loss of C from the rhizosphere is a rapid process and that microbial turnover of root exudates in the soil is very fast (Nguyen *et al.*, 1999; Kuzyakov & Cheng, 2001). When soluble C is added to the rhizosphere at ecologically realistic concentrations, rapid mineralization occurs with a half-life of between 0.5 and 2 h for most sugars, amino and organic acids (Ryan *et al.*, 2001). Considering the fast temporal dynamics of C within the plant, this suggests that C flow into and out of the plant-soil system can be extremely rapid with some compounds having a half life of between 3 h and 6 h in actively growing plants. In addition, some of the exuded C becomes incorporated into the microbial biomass, the turnover time of which is much slower (30–90 d). Based upon the results of Ryan *et al.* (1995) and Dilkes *et al.* (2004) amongst others, we can hypothesize that even the slightest change in the chemistry of the soil or physiology of the plant will induce rapid shifts in the quantity and quality of the exudative flux (e.g. changes in soil solution chemistry, grazing pressure, light intensity, temperature, etc.). Until now, research has tended to focus on the long-term effects of manipulating plants and soil on the quality and quantity of exudates. It is clear that further work is required to measure exudative fluxes at finer temporal resolution and to determine the impact of these on the soil microbial community, root processes and rhizosphere signalling.

VII. The role of root exudates in nutrient acquisition

Plants modify their environment at many spatial scales; the global, the ecosystem, the soil horizon, and the rhizosphere. In all ecosystems, plants transform the surrounding soil making and maintaining a habitat more favourable for growth (Marschner, 1995). Root mediated changes to the soil are mainly associated with ways to increase their potential for nutrient and water acquisition. Plants have evolved an array of mechanisms to increase the solubility, diffusion potential and uptake of nutrients from soil. These mechanisms are particularly important in low nutrient environments where plant demand can only be met by mobilizing nutrients from nonsoluble sources (Dakora & Phillips, 2002; Tables 1 and 2). There are two ways in which plants can enhance nutrient uptake from the rhizosphere, namely abiotic (i.e. chemical) and biotic, each of which will be discussed separately.

1. Abiotic mechanisms of nutrient acquisition

Directly or indirectly, growing roots alter their soil chemical environment. These changes occur as the result of a myriad of events including: water and ion uptake, exudation and uptake of protons and organic compounds, respiration (O_2 uptake and CO_2 release) and physical changes related to the speed of

Table 1 Possible functional role of root exudate components in the rhizosphere (adapted from Dakora & Phillips, 2002)

Component	Rhizosphere function
Phenolics	Nutrient source Chemoattractant signals to microbes Microbial growth promoters Nod inducers/inhibitors in rhizobia Resistance inducers against phytoalexins Chelators of poorly soluble mineral nutrients (e.g. Fe) Detoxifiers of Al Phytoalexins against soil pathogens
Organic acids	Nutrient source Chemoattractant signals to microbes Chelators of poorly soluble mineral nutrients Acidifiers of soil Detoxifiers of Al Nod gene inducers
Amino acids and phytosiderophores	Nutrient source Chelators of poorly soluble mineral nutrients Chemoattractant signals to microbes
Vitamins	Promoters of plant and microbial growth Nutrient source
Purines	Nutrient source
Enzymes	Catalysts for P release from organic molecules Biocatalysts for organic matter transformation in soil
Root border cells	Produce signals that control mitosis Produce signals controlling gene expression Stimulate microbial growth Release chemoattractants Synthesize defence molecules for the rhizosphere Act as decoys that keep root cap infection free Release mucilage and proteins
Sugars	Nutrient source Promoters of microbial growth

root growth. Consequently, parameters such as pH, redox, ionic strength, water potential, and the concentration of nutrients and organic compounds are different in the rhizosphere and the bulk soil (Tinker & Nye, 2000). Because of the different spatial scales of these processes (e.g. root exudation and ion uptake) and the different diffusion rates of solutes in soil, each position in the rhizosphere is chemically unique (Fig. 3). From an abiotic standpoint, the factors contributing most to enhanced nutrient uptake are plant induced changes in rhizosphere pH, redox potential, and metal complexation.

pH changes In many situations, the uptake of nutrients by roots leads to the release of H^+ into the soil to compensate for excess cation uptake (Sas *et al.*, 2001; Hinsinger *et al.*, 2003). This rhizosphere acidification is especially pronounced during the uptake of N in the form of NH_4^+. If the soil is acidic and N is taken up in the form of NO_3^-, the release of OH^- or HCO_3^- can occur leading to an increase in rhizosphere pH (Schubert & Yan, 1997). Although this has been postulated to reduce the toxicity of Al, Fe and Mn in acid soils (Runge & Rode, 1991), current evidence suggests that this may be of minor importance in comparison to other tolerance mechanisms (Ryan *et al.*, 2001).

In addition to the rhizosphere pH changes induced by cation–anion imbalance, other processes can also modify soil pH including: root organic acid release, root and microbial respiration, and redox-coupled pH changes (Hinsinger *et al.*, 2003). Although many carboxylic acids are released from roots, the primary acids contributing to pH shifts are citric, oxalic and malic acid (Jones *et al.*, 2003). While their release from roots has been intensively studied in crop plants under hydroponic conditions, the amount exuded by roots under field conditions remains unknown (see above). In the root cytoplasm (pH 7.1–7.4) these acids exist as anions (e.g. $citrate^{3-}$, $oxalate^{2-}$, $malate^{2-}$; Jones & Brassington, 1998). To maintain charge balance the release of these anions from the root must be counterbalanced by an influx of OH^- or efflux of cation (e.g. H^+, K^+). Electrophysiological characterization of root organic acid channels indicates that at least for the Al-induced, channel mediated release of malate, the counterion is K^+ (Ryan *et al.*, 2001). In most circumstances therefore, once the organic anions have been released from the root they can be expected to complex H^+ from the soil solution, raising the pH of the soil. Unfortunately, direct evidence to support organic acid-mediated alkalinization is lacking. Previously, it was almost universally accepted that organic acid exudation would significantly lower soil pH (Marschner, 1995). Most evidence for this has arisen from observations of strong acidification of the external root-bathing medium correlated with the main site of organic acid release (Hoffland *et al.*, 1989; Liang & Li, 2003). However, it is likely that this acidification is caused by an up-regulation of the plasma membrane H^+-ATPase and consequent H^+ release rather than acidification by organic acids (Neumann & Römheld, 1999; Ryan *et al.*, 2001). We speculate that up-regulation and co-ordination of H^+-ATPase activity with organic anion release serves a number of roles. Firstly, the H^+-ATPase will increase membrane potential providing a greater electrochemical potential gradient for channel mediated organic anion release. Secondly, the organic acid-stimulated mobilization of nutrients from the rhizosphere (e.g. P, Fe) is often greater when soil pH is lowered. The minor role of organic acids in rhizosphere acidification is supported by evidence showing that rates of H^+ release which could be achieved through organic acid exudation are two or three orders of magnitude lower than H^+ release via H^+-ATPase (Neumann & Römheld, 1999).

Table 2 The most important mechanisms for enhancing nutrient mobilization in the rhizosphere

	pH change	Redox change	Metal complexation	Biotic	Root morphology	Mycorrhizas
N				+ + +	+ + +	+ + +
P	+ + + ↘		+ +	+ + +	+ + +	+ + +
K						+ +
S				+ +		
Mg						+ +
Ca					+ + +	+
Fe	+ + ↘	+ + + ↘	+ + +		+ + +	
Mn	+ + + ↘	+ + + ↘	+ + +		+ + +	
B						
Cl						
Zn	+ ↘		+ + +		+ + +	
Cu			+ + +			
Mo	+ ↗					

+, low; + +, important; + + +, very important. The arrows show the change direction of the parameter for increasing availability of the nutrient.

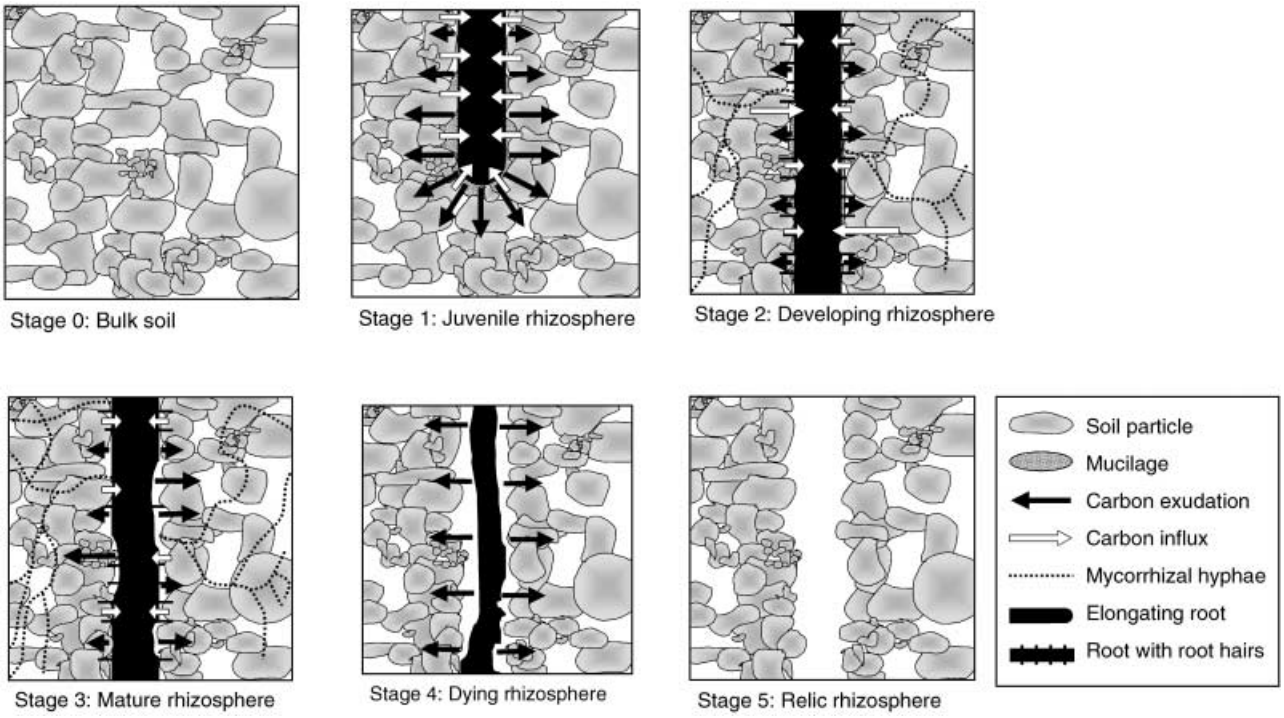

Fig. 3 Schematic representation of the developmental stages of the rhizosphere of an arbuscular mycorrhizal plant (e.g. grass or cereal root). We focus on the links between root development and C flow in the rhizosphere. Stage 0 represents the soil before the arrival of the root. Stage 1 represents the arrival of the root in which the exudation of soluble and insoluble (mucilage) C compounds is large compared to the rate of influx (exudate recapture and capture from surrounding soil). Exudation is maximal at the root tip and gradually declines further back along the root. Physical compression of the soil also occurs around the root. Stage 2 represents the developing rhizosphere in which root hairs are fully expanded and mycorrhizal infection has occurred. The rate of exudation is low and influx of C from patches in the soil is occurring (e.g. amino acids) as well as the active recapture of exudates. Stage 3 represents a mature rhizosphere whereby epidermal, root hair and cortical cell death is starting to occur. The mycorrhizal network is fully developed. Exudation is now large where root lysis is occurring. Influx is still active in areas with an intact epidermis. Stage 4 represents the dying rhizosphere where cortical cell death is widespread, mycorrhizas have been lost and C flow into the soil is large. The stele remains intact but influx is very low. Stage 5 represents a relic rhizosphere where the root has been completely decomposed leaving an impression channel in the soil. During the Stage 0–5 time series the microbial population will grow, will peak in Stage 3 and will then subsequently decline again towards Stage 5 where it will gradually revert back to Stage 0.

Rhizosphere respiration (comprising root and microbial respiration) may contribute to rhizosphere acidification. The extent of rhizosphere coupled pH decrease depends on the amount of CO_2 released and the amount of organic material oxidized to CO_2, as well as the initial pH of the soil (Hinsinger *et al.*, 2003). A range of ^{14}C and ^{13}C tracer studies have shown that approximately 5–20% of net fixed C can be accounted for in rhizosphere respiration (Hanson *et al.*, 2000; Nguyen, 2003). This equates to the release of 100–200 nmol CO_2 plant^{-1} s^{-1} (Durand & Bellon, 1994) or 50–200 nmol CO_2 g d. wt root^{-1} s^{-1} (van der Westhuizen & Cramer, 1998). Concurrently, it has been estimated that crop plant roots release between 10 nmol H^+ plant^{-1} s^{-1} or 2 nmol H^+ g d. wt root^{-1} s^{-1} from H^+-ATPases and other membrane transport activities (Durand *et al.*, 2001). This comparison shows that the rate of CO_2 released into the rhizosphere by roots and microorganisms is 10–100-fold greater than the H^+ required to satisfy the cation-anion imbalance (Hinsinger *et al.*, 2003). In a dissociated state H_2CO_3 would therefore decrease rhizosphere pH; however, as the first pKa of H_2CO_3 is 6.36 the contribution of rhizosphere respiration to acidification of most soils will be negligible with significant contribution only in neutral and alkaline soils.

Many chemical reactions occurring in soil involve the release and consumption of electrons. Because of the large demand for O_2 by roots and rhizosphere microorganisms, a large change in the soil's redox potential can be expected. Most redox processes are coupled with the release (oxidation) or consumption (reduction) of protons and therefore may cause pH changes. Two alternative situations should be distinguished when considering redox-coupled pH changes in the rhizosphere: for plants growing under normal, nonflooded conditions; and for wetland plants growing under low or negative soil Eh values. Under oxic conditions, the consumption of O_2 in root and microbial respiration decreases redox potential and, as a consequence, increases pH. For example, the reduction of one mole of Fe^{3+} consumes 2.5 mol of H^+; one mole of Mn consumes 3 mol of H^+; and one mole of NO_3^- to NH_4^+ consumes 6 mol of H^+, etc.

$$2FeOOH + CHO_2^- + 5H^+ \leftrightarrow 2Fe^{2+} + CO_2 + 4H_2O$$

$$MnO_2 + CHO_2^- + 3H^+ \leftrightarrow Mn^{2+} + CO_2 + 2H_2O$$

$$NO_3^- + 4CHO_2^- + 6H^+ \leftrightarrow NH_4^+ + 4CO_2 + 3H_2O$$

In these equations, formate (CHO_2^-) is used as an example of an organic substance. Such reduction processes have been suggested to be a strategy to acquire nutrients such as Fe and Mn by converting their insoluble oxidized forms into soluble reduced forms (Marschner & Römheld, 1994). These redox reactions show that under oxic conditions the most important reduction processes are coupled with a pH increase. By contrast, plants adapted to growing in flooded soils often transport O_2 from shoots to the roots via aerenchyma. Consequently, some of this O_2 is lost from the root causing the oxidation of Fe^{2+} to Fe^{3+}. In contrast to the reduction of Fe^{3+}, Mn^{4+}, or NO_3^- described above, the oxidation does not occur as a reverse reaction as electrons are supplied by released O_2. Nevertheless, protons are produced in this situation leading to a decrease of soil pH.

In summary, it is important to emphasize, that initial soil pH and soil buffering capacity are the most important factors regulating the direction and magnitude of the pH shift in the rhizosphere. Furthermore, the release of H^+, OH^- or organic acids from roots will depend largely on their environment and nutrient supply. Youssef & Chino (1989) clearly showed that barley and soybean alkalinized the rhizosphere if the initial soil pH was 4.8 and acidified the rhizosphere if the initial pH was 7.1. From this and other studies, it appears that the threshold soil pH defining the direction of the pH shift lies between 5.5 and 6.0 for most plants. Primarily, the magnitude of any pH change will depend on the soil buffering capacity which, particularly in calcareous soils, is very large (Hinsinger *et al.*, 2003). Of secondary importance is the form of N supply and therefore the balance of cation and anion uptake. Unbalanced cation uptake may lead to pH changes of about 2 pH units close to the root surface. We conclude that the release of organic acids, CO_2 and redox coupled pH changes are minor factors affecting rhizosphere pH.

Redox changes Shifts in soil redox status may affect the solubility of nutrients, not only by pH mediated changes as described above, but also directly. In particular, the solubility of Fe and Mn depends on the oxidation state of these elements and therefore on redox potential. In addition to the mechanisms of redox change described previously, plants have been shown to exude reduced organic compounds which can potentially increase Fe and Mn uptake (Marschner *et al.*, 1986; Römheld, 1987). As result of root exudation a reduction and enhanced dissolution of MnO_2 has been observed (Uren, 1982). This mechanism has been hypothesized to be particularly important under Fe and Mn deficiency in calcareous soils. Such reductases are thought to be exuded close to the root apex by most plants except *Graminaceae* (Uren & Reisenauer, 1988). While there is some evidence to suggest that this mechanism may be significant, direct field evidence is still lacking. Further work is therefore required to determine the molecular and physiological basis of the root exudation of these compounds. In addition, research is required to isolate and identify these compounds from a soil environment to see if greater concentrations can be found in the rhizosphere under plant deficiency conditions. Furthermore, comparison of the efficiency of this mechanism with other potential micronutrient acquisition strategies is warranted (e.g. phytosiderophores, Fe^{3+}-chelate reductase).

Under anoxic waterlogged soils, Fe^{2+} and Mn^{2+} can cause rhizotoxicity (Armstrong *et al.*, 1992). However, roots have been shown either directly or indirectly to induce the oxidation of Fe and Mn leading to the precipitation of Fe and Mn

plaques around the root. Such O_2 release around the roots could be viewed as a measure of adaptation of plants to grow under reduced conditions (Chen *et al.*, 1980).

Metal complexation in the rhizosphere Many of the compounds which can be lost from plant roots, have the capacity to form complexes with metal cations, mainly through carboxyl group interactions (e.g. organic acids, amino acids). This has led to considerable speculation that the formation of organometallic complexes in the rhizosphere could be of significance to the uptake of nutrients (e.g. K, Ca, Fe, P, Zn, Cu, Ni, Mn), with the notable exception of NO_3^- and NH_4^+. While many exudates can potentially indirectly enhance nutrient acquisition through activation of the rhizosphere microbial biomass, there are few instances where these mechanisms have been proven to be of direct significance in field environments. To a large extent this is because of the lack of available techniques, and the difficulties in performing rhizosphere experimentation in the field.

Many reports have demonstrated that plant nutrient supply regulates the amount and composition of root exudation with rates of exudation typically being enhanced under nutrient deficiency (Neumann & Römheld, 2001). However, most of these studies have been performed in hydroponic cultures under chronic deficiency conditions where a general breakdown in plant metabolism is occurring. Consequently, it is almost impossible to determine whether the response is under direct control of the plant, and part of a temporally co-ordinated and spatially targeted response to deficiency, or whether enhanced exudation is occurring as the result of a loss of membrane integrity over which the plant can exert little control. Furthermore, even if enhanced exudation is observed before chronic deficiency symptoms appear in hydroponic culture, the functional significance in a real soil environment remains unknown. Considering the differences in root morphology and physiology in roots grown in hydroponic culture and soil, major differences in root responses to nutrient deficiency may be expected.

At present, unequivocal evidence for the role of organometallic complexes in enhanced plant nutrient acquisition is sadly lacking. A good example of this concerns the controversy surrounding the role of organic acids in plant P uptake. It has been shown that under P deficiency, roots from a variety of plants release large quantities of organic acids such as malic, citric or pisidic acid (Hoffland *et al.*, 1989; Ae *et al.*, 1990). The magnitude of this response varies widely between plants, with exudation enhanced by 10–100-fold in P deficient lupins, whereas in most plants exudation is enhanced only 2–5-fold (Jones, 1998). After release, these organic acids can directly affect the behaviour of inorganic P in soil in a variety of ways: they can block P sorption sites in soil thereby enhancing the rate of P diffusion; they can directly displace P from sorption sites; they can complex metal cations on the sorption surface (e.g. Fe and Al in $Fe(OH)_3$ and $Al(OH)_3$, respectively) causing a loss of sorption site; and they can complex cations on mineral surfaces (e.g. Ca^{2+} in apatite), releasing P into solution (Jones, 1998). In addition, organic acids can bring organic P into solution which then becomes bioavailable (Gerke, 1993). There is evidence to support these potential mechanisms from *in vitro* studies where an organic acid solution is shaken with soil and P release into the aqueous phase measured. However, many of these *in vitro* experiments have used unusually high organic acid concentrations which do not reflect those predicted to exist in the rhizosphere (Jones, 1998). In addition, they have been performed in the absence of soil microorganisms which are known rapidly to degrade organic acids in soil (Jones, 1998). Even if the correct concentration range is employed, often the soil-to-solution ratio is very large and so the total amount of organic acid (nmol g^{-1}) can be 10–100-fold higher than would exist in the field. Consequently, in our opinion we feel that while many of these mechanisms may potentially be of significance, appropriate evidence to support them is completely lacking. One major issue to be resolved is the concentration of organic acids that exist in the rhizosphere. While mathematical modelling has indicated that concentrations at the rhizoplane will be in the range of 0.1–2.5 mM, these predictions are based upon exudation rates for root tips in solution culture (Jones *et al.*, 1996). It is conceivable that organic acid exudation in soil may be regulated at the cellular level whereby individual cells respond to external stimuli (e.g. P gradient from an apatite grain) causing highly localized patches.

There is therefore a real need to extend our current understanding of the role and behaviour of organometallic complexes in the rhizosphere. For obvious reasons there has tended to be an overemphasis on crop plants and therefore the role of organometallic complexes in natural ecosystems is lacking. Furthermore, we need to move towards more realistic experimental systems so that valid conclusions can be drawn about the significance of any observed findings. Previous results suggest that the behaviour of organic acids is very soil type dependent, with significant differences observed between calcareous and noncalcareous soils (Jones, 1998). Further research is therefore required to ascertain plant responses to different soil types. Further, the role of organic acids in P acquisition is often viewed in isolation from other potential mechanisms for increasing plant P uptake (e.g. mycorrhizas, root hairs, P transporter up-regulation, phosphatases, alterations in H^+-ATPase activity). We should not look at these root processes as a suite of co-ordinated responses to nutrient deficiency.

Metal complexation has been hypothesized to be an important mechanism in the enhanced solubilization of micronutrients in soil (e.g. Fe, Mn, Cu, Zn). While there appears to be strong evidence to support the role of root exudates in Fe uptake in monocotyledonous plants, the direct role of root exudates in the uptake of other micronutrients remains largely unsubstantiated (Bernards *et al.*, 2002). In the case of Fe uptake by

monocotyledonous plants, the release of phytosiderophores (nonproteinaceous amino acids) appears to play a crucial role in both the solubilization of Fe-containing minerals and Fe^{3+} uptake into the root. The release of these Fe-complexing agents is closely coordinated at a spatial and temporal level and is under direct genetic control (Cesco *et al.*, 2002; Rengel, 2002). Indeed, this is one of the rare instances where there is sufficient information from both soil and plant studies to give the mechanism credibility. In contrast, the uptake of Fe by dicotyledonous plants has been shown to involve the combination of a plasma membrane Fe^{3+}-reductase (reduces Fe^{3+} to Fe^{2+}) and a divalent cation channel which transports Fe^{2+} into the cell. Because of the insolubility of Fe^{3+} in soil, Fe^{3+} must be delivered to the root surface as an organometallic complex. It has been speculated that root exuded organic acids and phenolic substances may function as the carriers, however, although plausible, there is little evidence to support this. Evidence suggests that organic acid release and Fe-reductase activity are not spatially coordinated along the length of a root (Welch *et al.*, 1993; Ryan *et al.*, 2001), that organic acids are poor complexers of Fe under conditions typical of Fe deficiency (e.g. calcareous soils) and that many other potential Fe-complexing agents in soil are capable of being used. Much more work is required fully to elucidate the mechanism of Fe uptake in dicots and the role of root exudates in this process.

In acid soils, Al and Mn can inhibit root growth, reducing water and nutrient uptake and consequently diminishing plant productivity. However, some plants appear to be able to tolerate Al through the release of organic acids such as malate and citrate (Ma, 2000; Ryan *et al.*, 2001). This release is mediated by anion channels which are localized to the root tip where toxicity is manifest and are only triggered in the presence of Al. While this explanation of tolerance has drawn some criticism (Parker & Pedler, 1998), molecular and physiological evidence points towards it being realistic although whether it operates at an endo-(apoplastic) or ecto-rhizosphere level remains unknown (Ryan *et al.*, 2001). Further work is also required to demonstrate that organic acid release is the cause of plant Al tolerance in a field environment.

2. Biotic mechanisms of nutrient acquisition

Mechanistic studies of the role of root exudates in plant nutrient acquisition have usually been conducted in either hydroponic culture, quartz sand or sandy soils. Typically, sterile conditions are employed to prevent the biodegradation of root exudates. Under such artificial conditions, the microbial community around the roots, if present at all, is very small and can be expected to be unrepresentative of a normal rhizosphere microbial community. Despite the almost ubiquitous nature of mycorrhizas, very few mechanistic rhizosphere studies are performed in their presence. Consequently, the biotic mechanisms of nutrient mobilization in the rhizosphere are much less well understood than the abiotic mechanisms described above.

Biotic mechanisms of nutrient acquisition are predominantly based on mutualistic relationships between plants and rhizosphere microorganisms, mostly bacteria and fungi, as well as on the active search for nutrients by roots and proliferation of roots in nutrient rich soil patches (Hodge *et al.*, 1999). The mutualism with microorganisms is largely based on the release of labile, energy-rich C by the roots, and the consequent changes in the activity and structure of the microbial biomass around the root in comparison to the bulk soil.

Rhizosphere priming effects Organic substances released from roots not only provide an energy source for rhizosphere microorganisms, but also promote the chemotaxis of organisms towards roots (de Weert *et al.*, 2002). In some cases, the general growth of microbes in the rhizosphere may not be desirable as a result of possible competition for nutrients and also the likelihood of promoting the growth of pathogenic organisms. It is known that root exudation is an inevitable consequence of plant growth, and that many organisms are capable of moving towards and exploiting simple compounds such as sugars and amino acids. We hypothesize therefore that plants may recapture exudates lost into the soil to minimize the build up of deleterious microorganisms in the rhizosphere. However, there are clear examples whereby specific signals are released by the root in order to attract individual organisms. These compounds tend to be complex secondary metabolites which are released in small quantities into the soil in comparison to other exudate components. The best known example of this is the release of flavenoids by legumes and the attraction of rhizobia leading to the formation of root nodule and N_2 fixation (Jain & Nainawatee, 2002). The loss of C in this signalling mechanism is very small in comparison to the C invested in nodule formation and maintenance.

In more general terms, it has been hypothesized that rhizosphere microorganisms may accelerate the decomposition of soil organic matter (SOM) and also stimulate the dissolution of insoluble minerals in a way similar to that proposed for plants (pH, redox, and metal-complexation reactions; see above). This priming or 'microbial activation' of nutrient cycling is based upon a stimulation of microbial activity in the rhizosphere by labile C released by roots. According to Nobili *et al.* (2001), even very low amounts (μg g^{-1} soil) of some primers such as root exudates, may promote SOM turnover. This increasing mineralization of SOM has been linked to the increased demand for N by the soil microorganisms (Helal & Sauerbeck, 1986; Sallih & Bottner, 1988; Cheng & Coleman, 1990). The nutrients released from SOM may be rendered transiently unavailable to the plant, however, eventually these nutrients are made available upon turnover of the microbial biomass. This turnover is enhanced by faunal grazing (Ingham *et al.*, 1985; Clarholm, 1985a,b; Elliot *et al.*, 1988; Kuikman *et al.*, 1990, 1991; Griffiths, 1994; Alphei *et al.*, 1996). In quantitative terms, the role of this priming in both the long

and the short-term nutrient supply remains largely unknown. Although there appears to be little doubt that priming occurs in some soils, the downstream events leading from this and the overall benefit to the plant are complex. For example, as microbial growth in the rhizosphere is thought to be primarily N limited, root uptake of N could depress microbial growth and SOM turnover (Schimel *et al.*, 1989; Wang & Bakken, 1989, 1997; Ehrenfeld *et al.*, 1997; Bottner *et al.*, 1999). By contrast, if the SOM contains high amounts of easily decomposable C, the absence of N may stimulate the microbial decomposition of SOM. Alternatively, if two substrates with very different bioavailability (e.g. root exudates and SOM) are present at one location, microorganisms will utilize the easily available rhizodeposition before the SOM, resulting in a decrease in SOM decomposition (Sparling *et al.*, 1982; Billes *et al.*, 1988; Kuzyakov, 2002). Dormaar (1990) and Cheng & Kuzyakov (2004) concluded that biological rather than physical factors are responsible for rhizosphere priming effects and that microbial activation, preferential substrate utilization, and concurrence of demand for mineral N between plant roots and microorganisms, are the most important mechanisms of rhizosphere priming.

A critical point here is the nature of the C and N being exuded vs the quality of the C and N contained within the native SOM (Kuzyakov, 2002). It is clear that the balance of C supplied in sugars to N in amino acids (i.e. root exudate C : N ratio) is crucial, however, we have no knowledge of this ratio in soil. While there have been many studies of amino acids and sugars in root exudates, these are largely qualitative. Furthermore an in-depth knowledge of SOM cycling in the rhizosphere is also lacking.

Dissolved organic N cycling in the rhizosphere Traditional concepts of ecosystem N cycling have considered that organic N must first be converted to inorganic N (NO_3^- and NH_4^+) by microorganisms before plant assimilation (Marschner, 1995). This implies that roots and their associated mycorrhizas cannot directly take up organic N from soils (Nadelhoffer *et al.*, 1985; Norton & Firestone, 1996). However, recent studies in arctic tundra (Chapin *et al.*, 1993; Kielland, 1994; Schimel & Chapin, 1996), boreal forest (Näsholm *et al.*, 1998; Näsholm & Persson, 2001), alpine (Lipson *et al.*, 2001; Raab *et al.*, 1996, 1999; Miller & Bowman, 2003) and ericaceous ecosystems (Stribley & Read, 1980; Read & Bajwa, 1985; Read, 1991) have shown that plants can take up dissolved organic N (DON) directly from soils. Research on agricultural systems has shown that agriculturally important plant species, such as wheat (Näsholm *et al.*, 2000, 2001; Owen & Jones, 2001) and barley (Fokin *et al.*, 1993; Kuzyakov, 2002) can also take up DON from soils. Moreover, amino acid transporters in roots from a variety of plant species have been characterized at both the physiological and molecular level (Bush, 1993; Fischer *et al.*, 1995; Rentsch *et al.*, 1996; Tanner & Caspari, 1996). Although our understanding of amino acid cycling in the rhizosphere is well understood at a conceptual level, at a mechanistic level the flux and pool size of the components involved are not proven. Accordingly, the ecological significance of such processes are poorly understood, despite recent reviews which may suggest otherwise (Owen & Jones, 2001).

Current evidence suggests that the ability of plants to take up amino acids is a universal phenomenon which can take place in any terrestrial ecosystem (Fischer *et al.*, 1998; Persson & Nashölm, 2001; Wipf *et al.*, 2002). However, the contribution of this N uptake pathway relative to others remains controversial (Owen & Jones, 2001). We will concentrate therefore on ecosystems where the uptake of DON may be important, and the rhizosphere factors that may regulate the efficiency of this process.

The uptake of DON by plants has been demonstrated in cold ecosystems such as arctic tundra, alpine ecosystems and boreal forests where intrinsic rates of N mineralization are very low because of low temperatures and low pH conditions (Cao & Zhang, 2001; Jones & Kielland, 2002). Such ecosystems are more strongly N limited than others and soluble N is dominated by organic forms with correspondingly low concentrations of NH_4^+ and NO_3^- (Jones & Kielland, 2002). Evidence for a block in the N cycle comes from studies where low levels of inorganic N are detected in solution, implying low mineral N production rates. However, this does not always mean low rates of mineralization because such strong sinks for inorganic N exist that accumulation in solution does not occur. Although large concentrations of DON can be found in these soils, most of this is of a high molecular weight, recalcitrant nature and not directly available to plants (Jones DL & Kielland K, unpublished). Current evidence suggests that plants are only able to access low molecular weight DON such as amino acids, peptides and urea whose concentrations in soil are low. These low concentrations suggest that strong competition for low molecular weight DON exists in the rhizosphere (Owen & Jones, 2001; Bardgett *et al.*, 2003).

Studies from alpine ecosystems have demonstrated differences in the ability of plants to take up DON (Miller & Bowman, 2003), however, the mechanistic basis of these differences remain unknown. Possible explanations include species level differences in membrane transport activity, root distribution, N requirement, seasonal demands, and mycorrhizal colonization and root responses to different soil types (Chapin *et al.*, 1993; Falkengren-Grerup *et al.*, 2000). In addition, there are a number of soil factors which may indirectly influence plant uptake depending upon the mechanism of DON uptake (i.e. mycorrhizal or nonmycorrhizal mediated uptake) including rates of water flow, the amount of soluble inorganic N to DON and their relative diffusion rates. In addition, climatic factors such as soil temperature and moisture may control the forms of N in soil. NO_3^- usually dominates under high temperatures and high soil aeration conditions while NH_4^+ dominates under anaerobic conditions.

The contribution of DON to plant N acquisition has been estimated extensively under controlled conditions, but the true significance of organic N sources in plant nutrition has not been quantified in the field (Schobert & Komor, 1987; Chapin *et al.*, 1993; Kielland, 1994; Näsholm *et al.*, 2000, 2001; Lipson *et al.*, 2001). Most studies investigating DON uptake have been performed with the amino acid glycine, which may not always reflect the complex mixture of amino acids present in the soil solution (Näsholm *et al.*, 1998; Miller & Bowman, 2003). Hence, the current position is not whether plants possess the capacity for organic N acquisition, but rather the extent to which this capacity is realized in the field and how much it contributes to the annual N budget or life cycle of a plant. This implies that a full understanding of the role of DON in plant N supply can be achieved only if the physical, chemical and biological complexity of plant environment is intact (Näsholm & Persson, 2001).

If plants are using amino acids as a significant source of N, it implies that the rate of amino acid influx must exceed the rate of efflux. Conclusive evidence for this, however, is still lacking as typically only unidirectional influx is measured rather than net influx and comparative experiments with NO_3^- and NH_4^+ have rarely been performed under realistic field conditions (i.e. representative concentrations of amino acids, intact roots, etc.). Further, are these influx and efflux processes spatially coordinated along the length of the root? Again a full bi-directional flux balance with spatial analysis must be made before the uptake of DON can be proven to have ecological significance.

VIII. Mycorrhizal fungi and rhizodeposition

Mycorrhizal associations between a fungus and a plant root are widespread in the natural environment. The exact type of mycorrhizal association that forms depends upon both plant and fungal characteristics but the two most common types are the arbuscular mycorrhizal (AM) and the ectomycorrhizal association. There has been much research into how root exudates stimulate the formation of these types of association and the resulting alterations in exudation patterns following symbiosis establishment as discussed below.

1. Ectomycorrhizal associations and root exudates

Host root exudates can stimulate spore germination and mycelium growth of ectomycorrhizal fungi (Melin & Rama Das, 1954; Nylund & Unestam, 1982; Fries *et al.*, 1985, 1987; Ali & Jackson, 1988) although root exudates of several nonhost Brassicaceae have also been found to have a stimulatory effect on ectomycorrhizal fungi (Zeng *et al.*, 2003). In the presence of ectomycorrhizal fungi, quantitative differences in volatiles exuded from roots (Krupa & Fries, 1971) and qualitative differences in exuded compounds (Laheurte *et al.*, 1990; Leyval & Berthelin, 1993) have also been reported, but the significance and ubiquity of such alterations are unclear.

More specific associations can occur between certain ectomycorrhizal fungal species and host plants (i.e. the genus *Suillus* and *Rhizopogon* are conifer specific (Malajczuk *et al.*, 1982)) while 'broad host range' fungi which colonize a larger range of host species have also been recognized (Trappe, 1962; Molina & Trappe, 1982) suggesting that there are both general and more specific signalling compounds between symbionts. Chemotropism may play an important role in recognition events. Horan & Chilvers (1990) observed that when compatible fungal symbionts were separated from eucalypt roots by membrane filters the fungal hyphae were able to grow through the membranes and contact the host root apices. When the roots of several nonhost plants replaced that of the eucalypts no penetration of the membrane occurred. Furthermore, incompatible mycorrhizal fungi also failed to penetrate the membrane when eucalypt roots were present implying there is host specific stimulation of the mycorrhizal fungi. Also using eucalypts, Lagrange *et al.* (2001) found the flavonol, rutin, present in the root exudate had differing effects on ectomycorrhizal fungi at picomolar concentrations. Of the five *Pisolithus* strains tested, only two which had been collected under *Eucalyptus* spp. showed a rutin induced increase in biomass production. However, *Suillus bovinus* (not collected under *Eucalyptus* spp.) also responded to rutin while *Paxillus involutus* did not irrespective of it being collected from under *Eucalyptus* spp. or not. Two saprophytic fungi screened at the same time did not respond to rutin. This differing ability to respond to rutin may influence fungal populations in the rhizosphere of *Eucalyptus* spp. Cytokinins and indole-3-acetic acid (IAA), which are produced by the ectomycorrhizal fungi and the host plant, have also been found to affect ectomycorrhizal development (Gay & Debaud, 1987; Gogala, 1991; Gay *et al.*, 1994; Gea *et al.*, 1994) as has another fungal indolic compound, hypaphorine (Béguiristain & Lapeyrie, 1997; Ditengou & Lapeyrie, 2000).

Intriguingly, the formation of particular ectomycorrhizal associations may be further aided by mycorrhiza helper bacteria or MHBs (reviewed by Garbaye, 1994). MHBs have been suggested to either modify host root exudates or stimulate the host to produce different substances in order to enhance ectomycorrhizal formation by certain fungi (Garbaye, 1991). The MHBs themselves may also produce substances that stimulate certain ectomycorrhizal fungi either directly or indirectly by detoxifying harmful substances that would otherwise accumulate in the fungus and limit its growth (Fitter & Garbaye, 1994). The mechanism by which these MHB aid the growth of some species of ectomycorrhizal fungi while inhibiting others require further attention.

2. Arbuscular mycorrhizal (AM) associations and root exudates

Influence of root exudates upon AM formation Most current research into the impact of root exudation upon mycorrhizal

associations has been conducted on the AM symbiosis. This is probably because the AM association is the most widespread, occurring in about two-thirds of all land plants, and also because arbuscular mycorrhizal fungi (AMF) are obligate biotrophs with no method currently available for growing the fungus for any period of time in pure culture in the absence of a host plant. Thus, if the signals which encourage AMF to grow and develop could be deciphered then these culturing difficulties could be overcome. Although AM spores have been shown to germinate and produce small amounts of mycelium on agar and in soil, unless colonization of a growing root system occurs, hyphal growth will soon cease (Smith & Read, 1997). Following hyphal contact with the host root, appressorium formation occurs, colonization of the root cortex proceeds and arbuscules subsequently develop (Smith & Read, 1997). Although the results of some earlier studies suggest that root exudates may actually enhance AM spore germination (Graham, 1982; Siqueira *et al.*, 1982; Gianinazzi-Pearson *et al.*, 1989; Tsai & Phillips, 1991) it appears that the major influence of root exudates is to stimulate hyphal growth and branching rather than germination *per se*. Exudates may also have an attractional effect on AM hyphal growth in soil (Vierheilig *et al.*, 1998) which can be further modified by the internal P concentration of the plant as a consequence of the P-uptake efficiency of the genotype (Suriyapperuma & Koske, 1995).

Exudates from host plant species have frequently been reported to stimulate both hyphal growth and branching from germinated AM spores (Gianinazzi-Pearson *et al.*, 1989; Bécard & Piché, 1990; Nair *et al.*, 1991; Giovannetti *et al.*, 1993a,b) while those from nonhost plants do not (Glenn *et al.*, 1988; Gianinazzi-Pearson *et al.*, 1989; Buée *et al.*, 2000; Oba *et al.*, 2002). Moreover, this stimulatory effect is greater from host exudates released from P-stressed compared to P-sufficient roots (Amijee *et al.*, 1989; Nagahashi *et al.*, 1996; Tawaraya *et al.*, 1996; Nagahashi & Douds, 2000) and is produced constitutively rather than being induced by the AMF (Nagahashi & Douds, 2000). As exudate concentrations would be highest at the root surface this increased branching density may aid the fungus in making contact with the root and appressorium formation. Giovannetti *et al.* (1993a) found that while the exudates from the nonhost *Lupinus albus* did not inhibit growth of the AMF *Glomus mosseae* they did hinder hyphal attachment to, and appressoria formation on, the roots. The mechanism by which nonhost exudates influence AM development is contradictory. They may simply lack the compounds required to stimulate AMF (see Glenn *et al.*, 1985, 1988; Buée *et al.*, 2000) or release compounds which actively inhibit the fungus until through the formation of recovery branches the AMF is able to resume growth (Nagahashi & Douds, 2000; Gadkar *et al.*, 2003). A major difficulty when trying to determine the true significance and impact of exudates upon AMF is that studies differ widely in the experimental conditions used including duration of the study and exudate concentration and exposure time. Moreover the majority of these studies have been conducted in axenic conditions, thus the significance of the findings in soil is far from clear as exudates would have to make contact with the AM fungus at sufficient concentrations to evoke a response. As a result of the considerable activity of other microbes in the rhizosphere zone and their ability to utilize root exudates, this may be questionable.

The exact signals by which roots stimulate AM hyphal growth from spores or root fragments and enhance AM colonization is currently unknown. A wide range of compounds has been proposed to be involved including flavonoids (Gianinazzi-Pearson *et al.*, 1989; Chabot *et al.*, 1992; Bel-Rhlid *et al.*, 1993; Poulin *et al.*, 1993), volatiles (most notably elevated CO_2 concentrations: Suriyapperuma & Koske, 1995; Bécard *et al.*, 1992; Poulin *et al.*, 1993; Balaji *et al.*, 1995) and unidentified water soluble (Vierheilig *et al.*, 1998) or hydrophobic compounds (Tawaraya *et al.*, 1998). However, results from these various studies are contradictory. For example, although flavonoid compounds, particularly the flavonol, quercetin, have frequently been reported to be important signal compounds in this process (Gianinazzi-Pearson *et al.*, 1989; Chabot *et al.*, 1992) other studies suggest flavonoids are either not essential (Bécard *et al.*, 1995) or not involved at all (Buée *et al.*, 2000). The mechanism by which these signal compounds enhance hyphal branching is also unclear. Tamasloukht *et al.* (2003) recently demonstrated using the AMF *Gigaspora rosea* and *Glomus intraradices* that induced expression of fungal genes resulting in an enhanced fungal respiratory activity occurred just before increased hyphal branching. Other effects caused by the presence of root exudates that have been reported in the germ tubes of the AM fungus *Gigaspora margarita* include a more negative transmembrane electric potential difference (Ayling *et al.*, 2000), an increase in the cytosolic pH profile (Jolicoeur *et al.*, 1998) and an increase in fungal plasmalemma H^+-ATPase activity (Lei *et al.*, 1991). Such effects can be explained because of the transport of sugars and amino acids from the media (Jennings, 1995). Ayling *et al.* (2000) concluded that root exudates had a direct effect (rather than one mediated through gene expression) on the plasma membrane of *G. margarita* but clearly more comparative studies are required before it can be established which compounds present in root exudates are involved in enhanced hyphal growth and branching, by what mechanisms do they operate and if these differ among different AMF-host species combinations.

Influence of AM formation upon root exudates Following AM colonization, root exudation patterns may be expected to alter because the AM fungus is a considerable C sink (Douds *et al.*, 2000; Graham, 2000), AM colonization alters the carbohydrate metabolism of the roots (Shachar-Hill *et al.*, 1995; Douds *et al.*, 2000; Bago *et al.*, 2003) and increases root respiration (Douds *et al.*, 2000; Shachar-Hill *et al.*, 1995). Hyphal exudation from the AMF will also occur. Early studies

showed that plants grown under low P conditions increased exudation of amino acids, reducing sugars and carboxylic acids compared to plants grown under high P conditions although there was no change in the corresponding root content of these compounds (Ratnayake *et al.*, 1978; Graham *et al.*, 1981; Schwab *et al.*, 1983; Tawaraya *et al.*, 1994). This increased exudation was associated with changes in the membrane permeability of the low-P grown roots as measured by ^{86}Rb efflux (a measure of K^+ efflux; Ratnayake *et al.*, 1978; Graham *et al.*, 1981). Colonization by the AMF *Glomus fasciculatum* increased root P levels resulting in an enhanced root phospholipid content, a decrease in root membrane permeability and exudate release (Graham *et al.*, 1981; Mada & Bagyaraj, 1993). Although colonization by *G. fasciculatum* was correlated with root exudation patterns at the time of inoculation, being highest in P-deficient roots compared to P-sufficient roots (Graham *et al.*, 1981), the extent of AM colonization does not appear to be related to any specific exuded compound (see Schwab *et al.*, 1983, 1984). Similarly, other studies investigating a wide range of experimental factors (including light intensity, temperature, type and stage of development of plant species) upon AM development by *G. fasciculatum* have found increased colonization when root exudation was greatest (Ferguson & Menge, 1982; Graham *et al.*, 1982; Johnson *et al.*, 1982; Schwab *et al.*, 1984).

Qualitative changes in root exudation and rhizodeposition following AM colonization have also been reported (although not always; see Azaizeh *et al.*, 1995) including a reduction in total sugars (Ocampo & Azcón, 1985; Mada & Bagyaraj, 1993; Bansal & Mukerji, 1994), alterations in the composition of amino acids (Laheurte *et al.*, 1990; Mada & Bagyaraj, 1993), less K^+ and P release (Mada & Bagyaraj, 1993) and an increased release of nitrogen (including proteins), phenolics and gibberellins (Mada & Bagyaraj, 1993). It must be noted, however, that the consequences of such changes in the rhizosphere are seldom examined. Once roots are colonized by AMF, plants appear to be able to regulate further colonization through the exudates released. Root exudates from nonmycorrhizal cucumber plants enhanced hyphal growth from *Gigaspora rosea* spores while exudates from AM colonized plants did not (Pinior *et al.*, 1999). Moreover, AM colonization by *Glomus mosseae* was reduced in the presence of root exudates from AM colonized plants irrespective of the AM fungus present (*G. rosea*, *G. intraradices* or *G. mosseae*). Vierheilig *et al.* (2003) grew cucumber plants in a split-root system with only part of the roots exposed to, and colonized by, *G. mosseae*. When these exudates were added to further plants inoculated with AMF the exudates from both the colonized part and the uncolonized part of the root system failed to enhance root colonization and were even slightly inhibitory. By contrast, exudates collected from cucumber plants with no part of their root system exposed to AMF previously showed a stimulatory effect upon root colonization (Vierheilig *et al.*, 2003). Exudates released from AM colonized roots have also been demonstrated to reduce sporulation and zoospore production by *Phytophthora* species (Meyer & Linderman, 1986; Norman & Hooker, 2000), increase attraction of the plant-growth-promoting bacteria, *Azotobacter chroococcum* and *Pseudomonas fluorescens* (Sood, 2003), effect protozoan activities (Wamberg *et al.*, 2003) and alter microbial composition in the rhizosphere (Meyer & Linderman, 1986; Christensen & Jakobsen, 1993; Bansal & Mukerji, 1994). However, these effects are not consistently reported (reviewed by Hodge, 2000) and may depend upon other factors such as the growth phase of the plant (Wamberg *et al.*, 2003), nutrient availability (Green *et al.*, 1999) and the species of AMF present (Marschner *et al.*, 1997; Schreiner *et al.*, 1997).

3. Mycorrhizal associations, rhizodeposition and other considerations

In both the ectomycorrhizal and AM association the rhizosphere is extended into the mycorrhizosphere because the surrounding soil environment is not only influenced by the colonized root but the external mycelium of the fungal symbiont. The 'hyphosphere' is the term given to the soil influenced by the external phase of the mycorrhizal fungus. Through the release of compounds, mycorrhizal hyphae can influence microbial activity and nutrient dynamics in the hyphosphere soil, particularly ectomycorrhizal mycelium which is capable of releasing hydrolytic enzyme to acquire nutrients from organic sources (reviewed by Chalot & Brun, 1998), in addition to other compounds (Sun *et al.*, 1999). AM fungi can secrete large amounts of the glycoprotein, glomalin, into the soil environment (Wright & Upadhyaya, 1998; Wright, 2000; Rillig *et al.*, 2002, 2003), which may represent a recalcitrant pool of C in some soils (see Rillig *et al.*, 2001). Some of these exuded compounds may subsequently be reabsorbed by the mycorrhizal hyphae (see Sun *et al.*, 1999) just as roots can reabsorb exuded compounds (Jones & Darrah, 1993). Microbial activity and composition has been found to be affected in the hyphosphere of AM fungi (Andrade *et al.*, 1997; Filion *et al.*, 1999) although not always (Olsson *et al.*, 1996). Moreover, the rapid turnover of external hyphae, measured to be 5–6 d in the case of AM hyphae (although AM runner hyphae may persist for up to 30 d) represents a large input of carbon into the soil environment (Staddon *et al.*, 2003). Mycorrhizal colonization can influence rhizodeposition in other ways. For example ectomycorrhizal colonization increases root longevity (King *et al.*, 2002) while both increased and decreased root longevity has been reported following AMF colonization (Hooker *et al.*, 1995; Hodge, 2001; Atkinson *et al.*, 2003). The decomposition of the mycorrhizal root is also likely to differ from that of the nonmycorrhizal root because of the differing chemistry as a result of the fungus being present (see Langley & Hungate, 2003). Thus, rhizodeposition processes from mycorrhizal roots will differ markedly from nonmycorrhizal roots. How

different types of fungal symbionts affect rhizodeposition remains to be explored.

IX. Future thoughts

It should be clear from the arguments presented above that the rhizosphere is an extremely complex environment, the characteristics of which can be expected to vary dramatically with spatial location at an individual root, field, regional or global level (Fig. 1). Indeed, it is likely that we have seen only the tip of the iceberg of this multifarious environment particularly with regard to the biological interactions occurring in this zone of soil (i.e. signalling between roots and microbes and within rhizosphere microbial communities; Persello-Cartieaux *et al.*, 2003; Poole & McKay, 2003; Mantelin & Touraine, 2004). Furthermore, the ecological significance of most of the proposed interactions between root exudates and nutrients or metals in the soil remains unproven. For example, it is known that plants have a variety of mechanisms for enhancing P uptake from soil (Marschner, 1995). However, very rarely are experiments investigating the links between organic acid exudation and P deficiency performed on mycorrhizal plants. It may be expected that experiments performed in the absence of this almost ubiquitous symbiont may give misleading results. We must therefore move our attention away from studies in hydroponic culture towards experiments which use soil. This presents rhizosphere ecologists with major technical challenges; however, based upon progress in other areas of science these are not insurmountable. It is clear that advances in techniques such as isotopic labelling, NMR, microbial reporter gene technology, confocal microscopy, genomics, proteomics and metabalomics will all provide new opportunities to probe the factors that regulate rhizodeposition (Killham & Yeomans, 2001; Sorensen *et al.*, 2001; Kent & Triplett, 2002; van West *et al.*, 2003; Walker *et al.*, 2003). This review has also highlighted the need to provide better integration between plant physiology and molecular biology with soil chemistry, physics, and microbial and mesofaunal ecology. Working in isolation can still advance the field, however, the biggest advances will be made when scientific fields are integrated. This is exemplified by a recent study by Bais *et al.* (2003).

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