REVIEW ARTICLE

Rhizosphere: biophysics, biogeochemistry and ecological relevance

Philippe Hinsinger · A. Glyn Bengough · Doris Vetterlein · Iain M. Young

Abstract Life on Earth is sustained by a small volume of soil surrounding roots, called the rhizosphere. The soil is where most of the biodiversity on Earth exists, and the rhizosphere probably represents the most dynamic habitat on Earth; and certainly is the most important zone in terms of defining the quality and quantity of the Human terrestrial food resource. Despite its central importance to all life, we know very little about rhizosphere functioning, and have an extraordinary ignorance about how best we can manipulate it to our advantage. A major issue in research on rhizosphere processes is the intimate connection between the biology, physics and chemistry of the system which exhibits astonishing spatial and temporal heterogeneities. This review considers the unique biophysical and biogeochemical properties of the rhizosphere and draws some connections between them. Particular emphasis is put on how underlying processes affect rhizosphere ecology, to generate highly heterogeneous microenvironments. Rhizosphere ecology is driven by a combination of the physical architecture of the soil matrix, coupled with the spatial and temporal distribution of rhizodeposits, protons, gases, and the role of roots as sinks for water and nutrients. Consequences for plant growth and whole-system ecology are considered. The first sections address the physical architecture and soil strength of the rhizosphere, drawing their relationship with key functions such as the movement and storage of elements and water as well as the ability of roots to explore the soil and the definition of diverse habitats for soil microorganisms. The distribution of water and its accessibility in the rhizosphere is considered in detail, with a special emphasis on spatial and temporal dynamics and heterogeneities. The physical architecture and water content play a key role in determining the biogeochemical ambience of the rhizosphere, via their effect on partial pressures of O_2 and CO_2, and thereby on redox potential and pH of the rhizosphere, respectively. We address the

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various mechanisms by which roots and associated microorganisms alter these major drivers of soil biogeochemistry. Finally, we consider the distribution of nutrients, their accessibility in the rhizosphere, and their functional relevance for plant and microbial ecology. Gradients of nutrients in the rhizosphere, and their spatial patterns or temporal dynamics are discussed in the light of current knowledge of rhizosphere biophysics and biogeochemistry. Priorities for future research are identified as well as new methodological developments which might help to advance a comprehensive understanding of the co-occurring processes in the rhizosphere.

Keywords Soil strength · Soil structure · Water potential · pH · Redox potential · Nutrient availability

Introduction

Soils are the largest reservoir of biodiversity on Earth. They are important habitats for Prokaryotes and a diversity of Eukaryotes, which comprise fungi among soil microorganisms, as well as large variety of invertebrates (from protozoa and nematodes to mites, collembola, insects and earthworms). The diversity of Prokaryotes in soil has been estimated to be about three orders of magnitude larger than in all other environmental compartments of the Earth's ecosystems combined (Curtis et al. 2002; Crawford et al. 2005; Curtis and Sloan 2005). Roots of higher plants anchor the above-ground diversity of terrestrial ecosystems, and provide much of the carbon to power the soil ecosystem. Besides their role in biodiversity, soils are even more remarkable from a functional perspective, in sustaining all other forms of terrestrial diversity and providing many ecosystem services.

A major feature of soils is their temporal and spatial heterogeneities from the nm to the km scales (Young and Ritz 2000; Pierret et al. 2007). Soils are complex assemblages of extremely diverse habitats, which certainly explain why they harbour such a diversity of organisms. For instance, Ramette and Tiedje (2007) have shown that the interactions of environmental heterogeneities and spatial distance are central determinants of the relatedness and abundance of rhizosphere bacteria of the *Burkholderia cepacia* complex. Besides species richness, species abundances are also remarkable in soils (e.g. in Watt et al.

2006a). Even though a single gram of soil may contain about 10^7–10^{12} bacteria, 10^4 protozoa, 10^4 nematodes, 5–25 km of fungal hyphae, given an average specific surface area of about 20 m^2 g^{-1} and the very small size of most of these microorganisms, their surface coverage amounts in total to only 10^{-5}–10^{-6}% of the total soil surface area (Young and Crawford 2004). The soil can be considered a huge desert, where life is discretely distributed, even more so when one accounts for the tendency of many of these soil microorganisms to form colonies and to aggregate, forming hot spots of activity (Ranjard and Richaume 2001; Nunan et al. 2003; Watt et al. 2006b). One of the most fascinating hot spots of activity and diversity in soils is the rhizosphere (Jones and Hinsinger 2008).

The rhizosphere is best defined as the volume of soil around living roots, which is influenced by root activity (the "Einflusssphäre der Wurzel" according to Hiltner (1904) in Hartmann et al. 2008). As stressed by Hinsinger et al. (2005) and Gregory (2006) this means that, depending on the activity that one considers (exudation of reactive compounds, respiration, uptake of more or less mobile nutrients and water), the radial extension of the rhizosphere can range from sub-µm to supra-cm scales. As stressed by Darrah (1993), the inner boundary of the rhizosphere is not better defined. When one considers the movement of water, nutrients or endophytic microorganisms through the apoplasm, the inner boundary is inadequately represented by the outer surface of the root, as depicted in most rhizosphere models (Watt et al. 2006c). The temporal development of the rhizosphere is equally relevant to consider (Jones et al. 2004; Watt et al. 2006a and 2006c), although relatively poorly documented. Spatial and temporal components of the rhizosphere will thus especially be addressed in this review.

Soil is a physical environment where it is often difficult for roots, microorganisms and soil fauna to move, and where resources (water, air, nutrients) are frequently scarce and patchy, with considerable vertical variation down the soil profile. Even when abundant, soil resources are often poorly available to organisms due to the capacity of soil matrix to bind water and nutrients, so that roots have evolved to adapt and to influence their environment (Lambers et al. 1998; Raven and Edwards 2001; Hinsinger et al. 2005), optimizing their functional architecture to

explore and make use of resources in heterogeneous soils (Leyser and Fitter 1998; Pierret et al. 2007). Roots of higher plants (and their associated microbes) have coevolved with soils as they play a major role in soil formation processes, via a range of physical, chemical and biological processes (Verboom and Pate 2006; Lambers et al. 2009). The aim of this paper is to take the reader through a journey in the biophysical and biogeochemical environment of plant roots. In each topic we consider the ecological relevance, underlying processes and spatial/temporal heterogeneity operating in this crucial micro-environment.

Physical architecture of the rhizosphere

Ecological relevance

There are two fundamental reasons to attempt to understand the physical architecture of the volume of soil immediately surrounding the root. Firstly, the stability of this inner physical structure is a key determinant of a root's ability to explore and exploit the soil resource. Secondly, the geometry of the pore space (Fig. 1) defines the allocation of resources to soil biota, the permeability of gases and solutes to and from the root, and the diversity of microbial habitats in the area of highest carbon resource.

Underlying processes

For decades we have had at least a qualitative understanding of the impact of roots on the stability of soil. Simply put, the rhizosphere volume exhibits a greater resistance to an external, mechanical stress than soil not associated with roots, thus soil in the presence of roots generally exhibits greater stability. Typically this is assessed using some form of aggregate stability test (see Young et al., 2001) or rheological tests (Czarnes et al. 1999). Examining the influence of six crop species on aggregate stability Haynes and Beare (1997) found the presence of roots significantly increased stability (50–100% increase compared to a non-planted control), but only after the soil was air-dried. This result is directly related to the lower resistance of dry soil to slaking and highlights the importance of understanding the stability of soil systems across a range of environments. Additionally, legume crops were shown to have a greater influence on aggregation compared with non-legume crops. Overall, the authors attributed an important, yet undefined role, of the microbial community in increasing stability within plant species. In particular the role of saprophytic fungi in association with legume crops was identified as important. Caravaca et al. (2005) showed that a combination of plant type and rhizosphere microbial community affected aggregate stability. In their study arbuscular mycorrhizal fungi was implicated in increasing stability of soil associated with roots, which concurs with the work of Kabir and Koide (2000). In a recent study, Moreno-Espindola et al. (2007) found that root hairs were more important in the adhesion and stability of soil (predominantly sand –70%) than fungal hyphae. They reported a ratio of 40:1 for maize and 100:1 for Bermuda grass (*Cynodon dactylon* L.), even in the presence of arbuscular mycorrhizal fungi. The predominance of root hairs over hyphae may be due to the nature of the soil. Predominantly sand, this generates temporal changes in moisture (wet~dry cycles) occurring at the root-soil interface, which in addition to dense root hairs, increases stability and adhesion, as compared with soil more associated with hyphae. Soil-water is known to dramatically increase the cohesion and strength of sand – e.g. sand on a beach – and soil, through a mechanism known as effective mechanical stress (Mullins and Panayiotopoulos 1984).

Through many studies it is clear that biological activity may increase the stability of soil within and outwith the rhizosphere. What is evident is the importance of wet~dry cycles to 'lock-in' that stability. Clearly a combination of biophysical factors, the exact nature dependent on a wide range of conditions, impacts on the stability of soil at the root-soil interface. Another important factor relates to the chemical make-up of the carbon involved. Martens (2000) conclusively demonstrated the importance of phenolic acids, predominantly plant-derived, in soil aggregation. His works supports the conceptual framework of Tisdall and Oades (1992) that states "*residues with slower decomposition rates resulted in persistent soil aggregation*." Kaci et al. (2005), focussing on the production of exopolysaccharides by bacterial populations found exopolysaccharides exuded by *Rhizobium* to be composed of a tetrasaccharide repeating unit. This was considered as a thickening agent with polyelectrolyte properties which provided significant increases in soil aggrega-
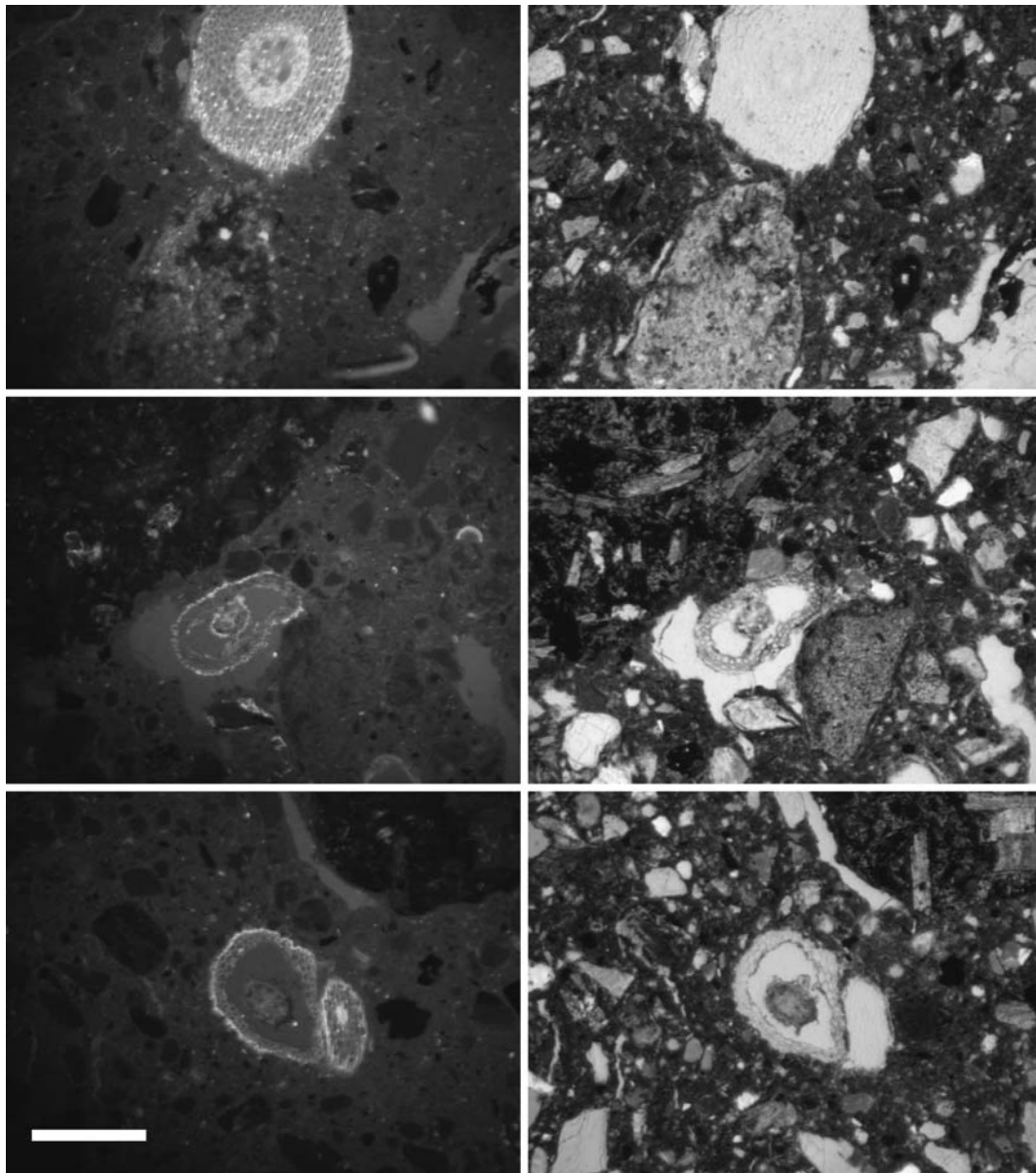
Fig. 1 Micrographs of soil thin sections showing barley roots growing in a sandy loam soil. Fluorescence images on left, transmission images on right. Images show a root with intact cortex in soil with few macropores present (top), a root with disintegrated cortex growing in a macropore (middle), and a main root axis with one of its lateral branches, distorted by the pressure of soil particles (bottom–only the lateral has intact cortex). Scale bar, bottom left, is 0.5 mm (Reproduced by kind permission of A. Glyn Bengough)

tion. Besides microbial exopolysaccharides, roots are also directly responsible for production of mucilages that altogether considerably affect soil structure in the rhizosphere and, ultimately structure-dependent processes such as water transport (Czarnes et al. 2000).

The combined effect of root hairs and mucilage either produced by the root itself or by rhizosphere microorganisms (Watt et al. 1993) can lead to the formation of specific structures called rhizosheaths (Fig. 2) which have been evidenced for a wide range of plant species and especially in grasses (Watt et al. 1994; Young 1995; North and Nobel 1997; McCully 1999; Moreno-Espindola et al. 2007). These structures are remarkably stable and play a dual role in

soil-root water transfers, whilst their formation is definitely linked with water dynamics (Watt et al. 1994; Young 1995). How stable a physical structure is, is obviously important in terms of the impact of external and internal perturbations on that structure. However, the geometry of the structure has a vital role in its functioning (Crawford et al. 2005). In the context of soil, the nature of the spatial and temporal geometry of the porosity is a key factor.

Gradients, spatial heterogeneity
and temporal development

Young (1998) provides a review of research in the variations of certain aspects of the geometry of soil

Fig. 2 Rhizosheaths formed around roots of *Lyginia barbata* R.Br. (top photograph) and barley (*Hordeum vulgare* L., bottom micrograph). Micrograph obtained by cryoscanning electron microscopy of the rhizosheath sampled in situ in field-grown barley plants. Development of long root hairs and their role in aggregating the soil thereby forming the rhizosheath is clearly visible (Reproduced by kind permission of Philippe Hinsinger (top photograph) and Margaret E. McCully)

from rhizosphere to bulk soil (i.e. soil without roots). A summary of his review shows a small but significant body of work that observed increases in bulk density close to the root-soil interface. This presents a picture of a root punching through soil, deforming and packing relatively wet soil to form the start of a new rhizosphere. Tighter packing around the root increases root-soil contact and thus, in theory increases hydraulic contact, and thus the probability of resource exchange from soil to root and vice versa. However, in front of the root tip any increase in density would be counter-productive. Slightly counter to this work is the research by Martens and Frankenberger (1992) on the impact of bacterial polymers which showed significant increases (20%) in porosity in pre-packed soils. In a similar vein Alami et al (2000) examined the role of exopolysaccharide-producing *Rhizobium* on the structure of rhizosphere soil, finding significant increases in soil porosity (12–60 μm), irrespective of initial soil water regime. An interesting secondary observation was the potential role of exopolysaccharides in reducing the impact of water deficit on plants. This neatly ties into the role of exopolysaccharides in minimizing the effects of desiccation on bacterial populations within biofilms.

In a recent study Feeney et al. (2006) carried out an extensive analysis of the impact of plant roots and microorganisms on the structure of the rhizosphere. Using a combination of high resolution x-rays and 3D geostatistical analysis they analysed micropore properties (>4.4 μm) from rhizosphere and non-rhizosphere soil. These results showed, for the first time in 3D, large and significant increases in micropore porosity associated with root+microbe, and microbe only soil, 12% and 8%, respectively compared with 4% in control. Such increased rhizosphere porosity does however not contradict increased bulk density, as reported by other authors when using techniques that do not resolve the pore size distribution with high resolution. Indeed root growth may result in larger pores being squashed to become smaller pores. Hence whilst the total porosity decreases (and thus the bulk density increases), the volume of particular size ranges of pores may actually increase, especially in the micropore range as reported within the rhizosphere aggregates as revealed by the use of high resolution x-rays and 3D geostatistical analysis.

Importantly, Feeney et al. (2006) also measured the spatial correlation that exists between pore volume

neighbours. This is an important measure as Crawford et al. (2005) and Young and Crawford (2004) suggest that as the spatial correlation increases this signifies a move from random to a correlated structure. The latter relates directly to an increase in local diffusion rates and thus resource allocation to the microsites where many of the microbial populations reside. This work provided the first substantive proof that soil-plant-microbe systems operate as a self-organised unit, with the microporosity as a driving force.

A key issue for future research related to the physical structure of soil, is to see a move away from relatively descriptive work (the physics of numbers and differences) to a more functional approach. It is less what is different and more what is the functional relevance of any changes in structure. Linking this into predictive models will provide a much needed input on the spatio-temporal dynamics of the soil system for all processes.

Soil strength in the rhizosphere

Ecological consequences of rhizosphere strength

The soil strength around the root apex greatly influences the pressure that a root must exert to penetrate the soil. If a pre-existing channel does not exist, a root must exert sufficient pressure to rearrange the soil particles and either push them aside, or ahead of the root apex. The soil within a radius of up to 20 times the radius of a penetrating probe can exert a mechanical influence on the probe (Greacen et al. 1969), and it is likely that this is also the case for a root. This is the zone where, depending on the soil mechanical properties, plastic (irreversible) and elastic (reversible) deformation occurs.

Mechanical impedance to root growth decreases the root elongation rate and increases root diameter (Taylor and Ratliff 1969; Bengough and Mullins 1990). Plants with shorter root axes explore a smaller volume of soil, and are therefore more likely to suffer nutrient and water shortage if these resources are scarce, limiting shoot growth. Mechanical impedance also restricts shoot growth directly, even when water and nutrient supply are non-limiting. Leaf expansion in young wheat seedlings decreased by two thirds as penetrometer resistance increased from 1.5 MPa to 5.5 MPa, and was unresponsive to increasing nutrient

supply (Masle and Passioura 1987). A rapid shoot response to mechanically stressing the root system was shown clearly by applying an external confining stress to roots of wheat (Triticum aestivum L.) and barley (Hordeum vulgare L.) growing in sand, causing decreased shoot elongation rates within 10 min (Young et al. 1997). This decrease in shoot growth associated with increasing soil strength is caused by an unidentified, and possibly complex, system of root-shoot signalling (Passioura 1988; Passioura 2002).

Plants growing in the field experience a wide range of soil physical conditions throughout a growing season (Bengough et al. 2006). Analysis of the strength of soil as a function of its matric potential indicates that mechanical impedance will often limit root elongation severely at matric potentials in the range −0.10 MPa to −0.25 MPa (Whalley et al. 2005a). Matric potentials in this range are not normally major limitations to root elongation in the absence of mechanical impedance (Sharp et al. 2004).

Soil strength also influences the colonisation of root tips by soil bacteria. Slower root elongation rates associated with compacted soil increased the numbers of bacteria in the rhizosphere around root tips of wheat grown in lab and field experiments (Watt et al. 2003). Watt et al. (2003) showed that root axes extending at one third of the elongation rate in loose soil had eight times as many bacteria and 20 times as many Pseudomonas spp. per unit length of root, with the biggest differences being in the apical 10 mm. The strength of the soil surrounding the root therefore has both direct and indirect effects on plant growth and rhizosphere ecology and, in the next section we consider some of the mechanisms influencing rhizosphere strength.

Underlying processes influencing rhizosphere strength

The mechanical properties of the rhizosphere depend on the local soil density, its matric potential, and the introduction of any materials that influence physical interactions between neighbouring soil particles.

The soil density in the rhizosphere will depend largely on the root diameter, and the path followed by the growing root tip. The total decrease in pore space around the root must be at least as big as the volume occupied by the root. The seminal root axes of most cereal crops rapidly approach their maxi-

mum diameter within a few mm of the root apex. Increasing soil strength decreases the length of the elongation zone of the root, and can as much as double the root diameter (Bengough and Mullins 1990; Watt et al. 2005). The trajectory followed by a root tip will depend on the spatial variation in soil strength. For instance, roots often locate and occupy large channels in the soil more frequently than expected by chance alone (Stirzaker et al. 1996). Indeed, 80% of wheat roots were found within 2.2 mm of soil macropores, in two Australian vertisols (Stewart et al. 1999). The mechanism whereby roots locate such pores may well be linked to circumnutation (the spiralling pattern of root growth), that has been observed since Darwin in humid air and in relatively soft media such as agar. Circumnutation has been found to interact with gravitropism and the mechanical properties of the growth medium, to produce a waving pattern of root growth in *Arabidopsis*, even on a simple gel surface (Thompson and Holbrook 2004). The stress regime around a growing root tip will be complex, but cracks and fissures in the soil may represent low resistance pathways for root growth, that are detected when they come within a few root diameters of the root tip.

The matric potential of the rhizosphere becomes more negative as roots extract water from the soil. As soil strength may increase by >100 fold as soil dries from −1 kPa to −1.5 MPa, the pattern of water extraction in the rhizosphere will greatly influence soil conditions (Whalley et al. 2005a). It is also reasonable to assume that water, transported via hydraulic lift through the root system from deeper roots growing in wet soil, and released into drier surface soil at night, when the transpiration demand is minimal, will decrease rhizosphere strength in the upper portion of the soil profile. Similarly, if the water potential of mucilage released by the root cap is more positive than the matric potential of rhizosphere soil, this may soften the way for a penetrating root (Passioura 2002). Feedback between rhizosphere strength and exudation results in greater release of root exudates by mechanically impeded roots (Barber and Gunn 1974; Boeuf-Tremblay et al. 1995). Barley plants grown in glass beads released approximately twice the dry mass of exudates as compared with plants in liquid culture, with maize (*Zea mays* L.) exuding a nine-fold greater mass of carbohydrate (Barber and Gunn 1974). Boeuf-Tremblay et al.

(1995) demonstrated that this was due to root exudates rather than rhizosphere microbial products as they observed an increased exudation with increasing strength in axenically-grown maize seedlings. Such a large release of exudates into the rhizosphere may well give rise to the greater numbers of bacteria observed around the tips of mechanically impeded roots in soil (Watt et al. 2003).

The increase in exudation with an increase in soil strength is also accompanied by an increase in the release of root border cells per mm of root elongation (Iijima et al. 2000). A 12-fold increase in border cells/ mm root elongation was measured for maize radicles in compacted, as compared with loose sand. The number of border cells released was sufficient to cover completely the surface of the root cap in compacted sand, decreasing the frictional resistance to root penetration and acting as a lubricating sleeve around the root tip. This disposable sleeve of cells may decrease the colonisation of the root tip by bacteria. Indeed both frictional resistance and bacterial colonisation of the root tip increase markedly if the root cap is removed from maize (Iijima et al. 2003; Humphris et al. 2005). Relatively little is known about border cell release in older plants, and there is interesting new evidence that border cell release may decrease substantially with increasing root age (Odell et al. 2008). Both border cells (Fig. 3) and root cap mucilage may lubricate root penetration (Iijima et al. 2004), and there is evidence that enhanced root exudation in mechanically impeded roots persists and even increases with plant development stage (Boeuf-Tremblay et al. 1995).

Gradients, spatial heterogeneity and temporal development

Gradients in rhizosphere strength depend on the associated gradients in soil density, matric potential, and root deposition of organic material. The mechanical stress in the soil around the root tip is likely to be greatest immediately in front of the root apex; the distribution of stress simulated using a Finite Element Model was changed by thickening of the root tip such that a 60% increase in the root diameter decreased the peak axial stress in front of the root tip by a quarter, facilitating root penetration (Kirby and Bengough 2002). Deformation of the rhizosphere will be greatest where roots have historically exerted most mechanical
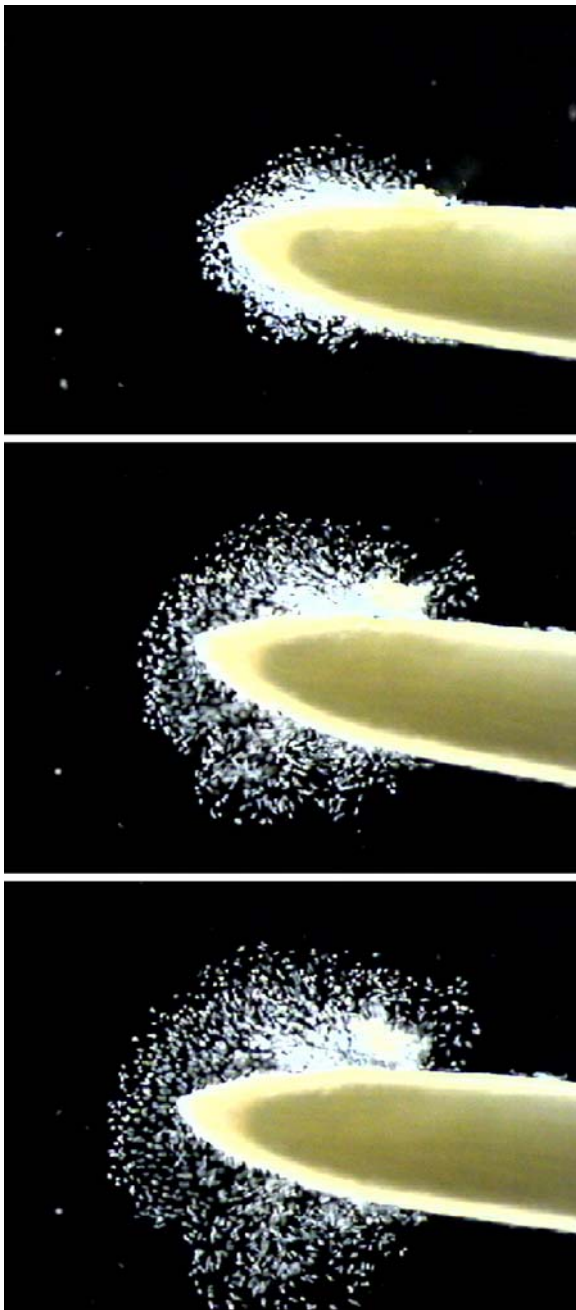
Fig. 3 Timelapse sequence of border cell release during mucilage hydration following immersion of a maize (*Zea mays* L.) primary root tip in water, after 1, 3, and 9 min. Maize root diameter is approximately 1 mm (Reproduced by kind permission of A. Glyn Bengough)

stress on the surrounding soil. Such deformations can be large and estimates of local density around maize roots indicate dry bulk densities as great as 1.8 g cm^{-3} next to the root surface, as compared with 1.54 g cm^{-3} in the bulk soil (Bruand et al. 1996; Young 1998). The variation in soil porosity has been modelled as decreasing exponentially away from the root surface (Dexter 1987), although this form of model is derived mainly from empirical fits to the data available, rather than to a mechanically based model.

The local physical environment of a root can be influenced greatly by the presence of root channels from preceding crops, especially in hard soils (e.g. maize following the tropical legume *Stylosanthes hamata*, Lesturgez et al. 2004). This is illustrated clearly by minirhizotron images showing soybean roots growing along channels in compact soil left by decomposing roots of canola just 2 to 3 months earlier (Williams and Weil 2004). In similarly dense soils that were unploughed, more than half of the entire length of wheat root systems contacted the decaying skeletons of roots (Watt et al. 2005). Such a large local input of root material is likely to greatly alter the local environment within the macropore sheath – the zone of soil typically within 1 to 3 mm of the macropore wall (Stewart et al. 1999). Indeed, the fungal and bacterial populations within the macropore sheath can be greatly enhanced in comparison to those of the bulk soil (Pierret et al. 1999), even more so than these authors found in the rhizosphere of the same soil after repacking. Bundt et al. (2001) also showed that preferential flow paths in soils were to be considered as biological hot spots, possibly because of being sites of deposition of organic matter and nutrients. This is especially the case for biopores such as earthworms galleries and root channels, i.e. either present day or relic rhizospheres (Pierret et al. 2007). While penetration of root systems to depth will enable roots to access valuable reserves of water deep in the subsoil, clustering of roots within relatively sparse macropore channels means that the extraction of water from large blocks of subsoil may be relatively much slower than if the roots were uniformly distributed throughout the subsoil volume (Passioura 1991).

Water distribution and accessibility in the rhizosphere

Ecological relevance

Water is the solvent and transport medium in natural systems. Water is a major constituent of plants and

microbes and a reactant or substrate in many important processes crucial for metabolic activity. Another role of water is the maintenance of turgor which is essential for cell enlargement and growth (Kramer and Boyer 1995). However, most of the water taken up by plants is transpired to the atmosphere in their attempt to assimilate CO_2 (Jackson et al. 2000).

Roots provide the hydraulic continuity between soil and atmosphere and thereby play a key role in the global water cycle. Water lost through stomata during photosynthesis has to be replaced by uptake from the soil. As discussed above, with decreasing water content in soil its mechanical resistance increases and penetration of roots is hindered (Pardales and Kono 1990, Sharp and Davies 1985). In dry soils roots (fine roots in particular) may desiccate and loose their function. Nutrient uptake is reduced due to decreasing nutrient mobility and vanishing uptake capacity (root activity). Resources in dry soils are not available to the plants and the associated micro-organisms, thus competition for the limiting resources increases if parts of the soil dry. The ability of some roots to continue elongation at water potentials that are low enough to inhibit shoot growth completely is an important species specific response to soil drying (Sharp et al. 2004). Plant species able to maintain root activity and growth in drying soil or to compensate the uptake of nutrients and water by other parts of the root system or by an association with microorganisms which help to overcome the negative effects of soil drying may have a competitive advantage under water limiting conditions. Such differences between plant species in certain traits may determine community composition in natural ecosystems but also the efficiency of intercropping system in agriculture or agro forestry (Callaway et al. 2003).

Soil micro-organisms are predominantly aquatic in nature, i.e. are living in the liquid phase and not in the air-filled pores. Key aspects of moisture in the rhizosphere include the matric potential which deter-mines the distribution of water-filled pores (providing hydraulic connectivity) which in turn act as valves in soils altering the diffusion rates of gases to and from microbial populations (Focht 1992). This regulates the activity of aerobic against anaerobic organisms (Young and Ritz 2000). It is important here to draw a distinction between an anaerobic environment which exists due to say a pore being filled with water, and a pore separated from other pores due to say annular water rings held by capillary action onto organo-mineral surfaces surrounding it.

Additionally, the matric potential regulates the thickness of the water films adhering to organo-mineral surfaces. This is again linked to the hydraulic connectivity of soil pores, and directly impacts the movement of bacteria and protozoa. At a higher order, nematode movement has been shown to be intimately linked to water-film thickness (Wallace 1958), which has been recently shown to be implicated in potential gene flow and the creation of biodiversity.

An important aspect of microbial activity in the rhizosphere is the ability of microbes to adapt to a highly varied moisture regime so close to a major sink of water; and of course under some circumstances, for instance hydraulic lift, an important source of water.

Underlying processes

Root water uptake in the soil-plant-atmosphere continuum is a passive water flux driven by the water potential gradient between the soil and the atmosphere. It can be regulated by stomatal movement, but for open stomata it is a function of the potential gradient and the conductivity/resistance in the system.

In older textbooks, roots are regarded as nearly prefect osmometers. Clarkson et al. (1971) and Sanderson (1983) showed higher uptake fluxes in the younger regions of the root of barley and related it to the endodermis development in older regions of the root. Although water flow through the root cortex can occur in parallel pathways, through the apoplast (cell walls), through the symplast (plasmodesmata) or transcellular (aquaporins), it was indeed assumed for a long time that the endodermis with its casparian bands stops apoplastic flow completely and thus acts as the 'root membrane' (Passioura and Munns 1984, Steudle and Peterson 1998). This classical view was challenged in recent years as there are numerous indications for an apoplastic bypass through the endo-dermis. Casparian bands are not yet developed in some areas like root primordia and root tips and, in addition, casparian bands are not absolutely impermeable to water as analysis of the isolated material has shown (Schreiber et al. 2005, Zimmermann et al. 2000). This, results of puncturing experiments in which the effects of small holes in the endodermis on hydraulic con-ductivity were measured (Steudle 1993), and detailed measurements with root and cell pressure probes of

root and cell hydraulic conductivities and reflection coefficients, led to the development of the 'composite transport model', i.e. parallel pathways for water uptake with different relevant driving forces occurring also across the endodermis (Steudle 2000, 2001).

Along the apoplastic path, water movement will be hydraulic in nature, i.e. driven by gradients in hydrostatic potential. Cell walls have no selective properties for solutes (reflection coefficient σ is close to zero), thus osmotic gradients are not relevant for this path.

Along the cell-to-cell path (plasmodesmata and aquaporins) the reflection coefficient σ, a measure for the semi-permeability of a membrane, is close to one and hence osmotic and hydrostatic potential gradients act together in an additive manner.

The relative contribution of hydraulic (predominantly apoplastic pathway) and osmotic (only cell-to-cell path) flow to total water flux changes with root development (Frensch et al. 1996) and environmental conditions (Vandeleur et al. 2005).

The hydraulic conductivity (or its reciprocal, the resistance) differs between the two pathways. It has been shown in numerous measurements, especially for tree roots, that the conductivity for the hydraulic flow can be up to three orders of magnitude greater than for the osmotic flow (Steudle and Peterson 1998). The hydraulic conductivity in either pathway is not constant but changes with maturation of root tissue and number and function of aquaporins (Frensch and Steudle 1989; Frensch et al. 1996; Barrowclough et al. 2000; Tyerman et al. 2002; Vandeleur et al. 2005). Changes based on aquaporin expression can occur within hours and result in diurnal fluctuation of hydraulic conductivity (Henzler et al. 1999). Similarly, diurnal fluctuations in root diameter have been observed in rhizotron studies, and may give rise to large changes in root-soil contact for roots located in macropores (Huck et al. 1970). Any decrease in root-soil contact will decrease the hydraulic conductivity of the root-soil interface, although there is evidence that frequent exposure to water deficit may harden roots, decreasing such fluctuations in diameter during drying cycles (Lemcoff et al. 2006).

A important highlight in any discourse on soil water is an explicit recognition that, generally the root and microbes are living in and adapting to a complex mix of solutes that make up soil moisture, and our general notions of the simplicity of soil 'water' fail. A growth area in research is directly related to microbes'

ability to alter the surface tension and contact angle of soil moisture (Urbanek et al. 2007). This will have important implications for the shape of the moisture characteristic and the sorptivity of soil, which of course feeds forward to a wide range of important processes.

The presence of mucilage in the rhizosphere has given rise to studies on its ability to retain water. The first of these studies used freezing point depression (Guinel and McCully 1986), and may well have been flawed due to the difficulty of using this technique with a gel (McCully and Boyer 1997). Later studies using thermocouple psychrometry suggested that maize mucilage may contain 99.9% water at potentials of −50 kPa (Read et al. 1999), although under wetter conditions the mucilage contained even greater quantities of water (McCully and Boyer 1997).

Surfactants, such as lecithin, contained in mucilage may change the water-release properties of the rhizosphere, such that more water is released, especially from relatively wet coarse textured soils (Read et al. 2003). Measurements of the water-release characteristic of the rhizosphere, as compared with bulk soil, showed that rhizospheres of barley and maize were drier than bulk soil at the same matric potential, partly as a result of changes in rhizosphere pore-size-distribution and angle of wetting (Whalley et al. 2005b). Besides hydrophilic substances, hydrophobic compounds can also be produced by either roots or microbes, resulting in increased water repellency in the rhizosphere relative to bulk soil (Czarnes et al. 2000; Hallett et al. 2003), which further complicates the biophysics of the rhizosphere.

Gradients and spatial heterogeneities and their temporal development

The site of maximum water uptake along a root is determined by the interplay between radial root resistance (see above) and axial root resistance and can be compared with hydraulics in porous pipes (Zwieniecki et al. 2003). Axial resistance is a function of xylem maturation and xylem vessel diameter as well as number and organisation of xylem vessels (Shane et al. 2000, Steudle and Peterson 1998). These traits are highly species specific, but are altered by environmental conditions (Tyree and Sperry 1989). While axial conductivity increases with increasing distance from the tip as xylem vessels are formed and mature, radial conductivity decreases due to formation

of endodermis and exodermis with casparian bands and suberin lamellae. For fully differentiated root tissue axial conductivity is larger by orders of magnitude than radial conductivity.

For barley (*Hordeum vulgare* L.) and pumpkin (*Curcurbita pepo* L.) the maximum water uptake was reported to occur 3–8 mm behind the root tip (Clarkson et al. 1971; Sanderson 1983; Kramer and Boyer 1995). For tree roots maximum uptake was observed close to the root tips or where lateral roots are emerging (Häussling et al. 1988). Clearly, non-invasive techniques such as magnetic resonance imaging, X-ray computer tomography or neutron radiography which enable visualizing roots and water in soil simultaneously (Fig. 4), bear a great potential for investigating water uptake profiles along single roots (MacFall et al. 1990; Pierret et al. 2005; Menon et al. 2006). However, despite recent technological advances, non-invasive observations of plant roots and their environment still face a trade-off between spatial resolution, field-of-view and three-dimensionality (Pierret et al. 2003; Garrigues et al. 2006).

Gradients in soil water content may not only develop along a root as a result of different uptake rates but may also develop radially around a root if soil hydraulic conductivity becomes limiting for uptake (Fig. 5). This is likely to occur under high evaporative demand, a small root-shoot ratio and a

coarse soil texture (Gardner 1960; Sperry et al. 2002) and was demonstrated experimentally (Hainsworth and Aylmore 1989; MacFall et al. 1990). Such gradients in soil water content or soil matric potential are taken into account in microscopic approaches of modelling plant water uptake and can there function as a threshold. This is in contrast to macroscopic models on plant water uptake in which roots are only regarded as a diffuse sink which varies in size as a function of soil depth (Feddes et al. 2001). Recently Doussan et al. (2006) have combined models describing explicitly root architecture (root system growth and deployment in space) with the microscopic approach of describing water uptake based on potential gradients in soil-plant-atmosphere continuum. With this approach they were able to reproduce the water distribution patterns obtained in experiments.

Gradients in soil water content develop around roots, along developing roots but also on a larger scale between different soil horizons. Root distribution throughout the soil profile varies with plant development (annual crops) season and plant species and shows an extremely high plasticity, i.e. is not only genetically controlled but adapts to environmental conditions (Callaway et al. 2003). Likewise water is not distributed evenly throughout the soil profile even under equilibrium conditions, due to the shape of the water retention curve and the effect of gravity. As a consequence the contribution of different soil horizons to cover evaporative demand shows a large fluctuation and changes with time. In regions with seasonal precipitation patterns topsoil, where the highest rooting density prevails, usually dries up first, but deeper roots may tap ground water or soil layers close to the water table showing little fluctuation in water content.

Roots may partly buffer such large scale gradients by redistribution of water from wetter soil regions to drier regions of the soil profile. Water is released from roots during periods when transpiration ceases (usually at night) and soil water potential in the dry soil region becomes more negative than plant water potential. This phenomenon, also known as 'hydraulic lift' has been shown to exist in about 30 different plant species and the reported amounts of water transferred per night range from 14 to 30% of daily evapotranspiration. However, despite its potential importance for water use efficiency, facilitation or water parasitism, nutrient uptake from dry topsoil or maintenance of root function, the magnitude, path-

Fig. 4 Volumetric water content [%] distribution along 3 week old tap root of lupin (*Lupinus albus* L.) growing in a sandy soil obtained by neutron radiography (performed at the facilities of Paul Scherer Institute, Zürich). The root, due to its high water content, shows up as a longitudinal body in the centre. The field of view of the picture is ten by 40 mm, it is a detail of a neutron radiogram with an original field of view of 150×150 mm, pixel size is 0.272 mm. The scale from red to blue corresponds to volumetric water content ranging from 40 to 28% (Reproduced by kind permission of Andrea Carminati et al.)
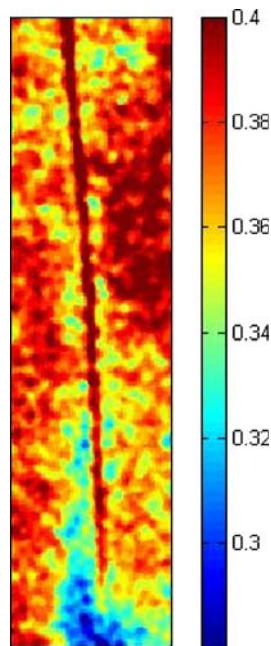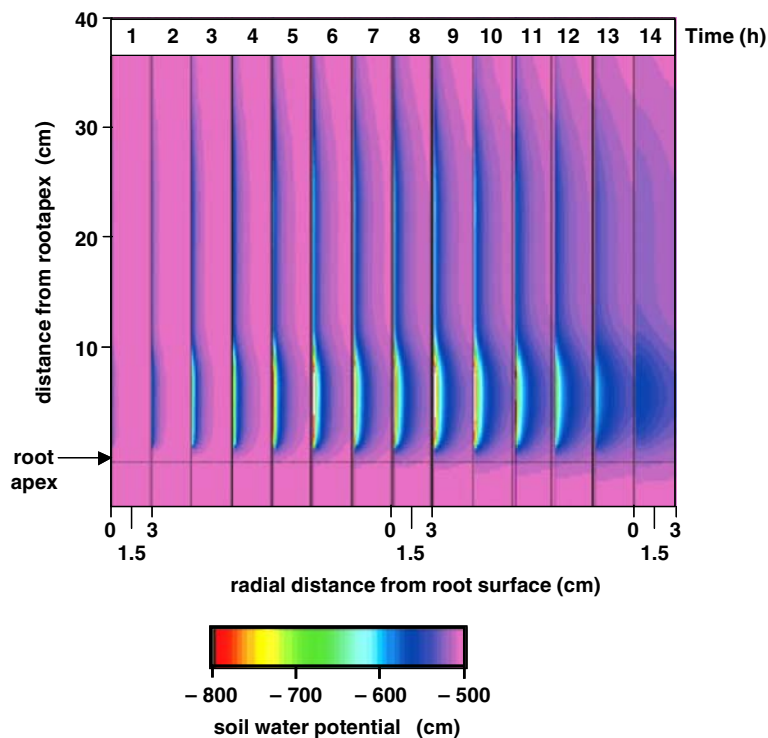
Fig. 5 Temporal development of radial and longitudinal gradients of water potential as a consequence of water uptake by a root of maize (*Zea mays* L.) growing in a clay loam at an initial soil water potential of −0.05 MPa (equivalent to 500 cm water column), as obtained by modelling. The root axis is located along the left axis of each box. In order to account for the day/night cycle of transpiration, a sinusoidal variation (between −0.1 and −1.2 MPa) of the xylem water potential was imposed. Axial and radial variations of the hydraulic conductance along the root were included in the simulation and generated an heterogeneous pattern of uptake and water potential in the soil along the root, with greater variations near the root tip (Reproduced from Doussan et al. (2003) by kind permission of EDP Sciences)

ways and resistances of these redistribution processes are still poorly understood (Caldwell et al. 1998; Callaway et al. 2003; Newman et al. 2006).

It is well proven by direct measurements that water can move in either direction within the root system depending on the direction of water potential gradients (Burgess et al. 2000) and there is no indication of a general "rectifier like behaviour of roots", i.e. a higher resistance to water efflux compared with influx, from anatomical or physiological features. However, root radial resistance can increase by formation of suberin lamellae in the tangential walls in the exodermis or dehydration of root tissue, resulting in a decrease of root radius and increased formation of an air gap between the root surface and the soil, i.e. a loss of root-soil contact (Nobel and Cui 1992). For a long time it is known that variation in root diameter occurs reversibly on a diurnal basis (Huck et al. 1970). Consequences of changes in root

diameter for root-soil contact are described in detail by Veen et al. (1992).

Whether hydraulic redistribution is observed in measurable quantities not only depends on root resistance but also on hydraulic conductivity of the soil (Vetterlein and Marschner 1993). Hydraulic redistribution was observed less frequently in coarse textured soils than in fine textured ones (Yoder and Nowak 1999). Another important factor for hydraulic redistribution, apart from the size of the water potential gradient between the wet and dry soil regions, is the ratio between the uptake capacity in the moist region and the density of functional roots in the dry region (Ryel et al. 2002).

Last but not least the presence of salt, decreasing osmotic potential, may affect water redistribution. Salts can accumulate around roots and thus, as for soil matric potential, steep gradients for osmotic potential can be formed around roots (Stirzaker and Passioura

1996; Vetterlein and Jahn 2004a). Whether and to which degree salts accumulate depends on initial salt concentration in soil solution, soil texture and the ratio between evaporative demand and plant requirement for the ion in question (Vetterlein et al. 2004, 2007a). The extent to which water uptake is reduced due to such gradients in osmotic potential depends on the relative contribution of osmotic and hydraulic flow to total water uptake and thus varies with environmental conditions like evaporative demand. Likewise plants growing in saline soils can adjust osmotically to salinity and this may constrain water release to drying soil.

Chemical ambience (pH and redox potential) of the rhizosphere

Ecological relevance

The soil pH has dramatic importance for below-ground life. One of the most striking pieces of evidence is shown by recent biogeographical studies, e.g. Fierer and Jackson (2006) study which investigated a data set of 98 soils sampled across the Americas. This study showed that temperature, rainfall and latitude had virtually no effect on the diversity and richness of soil microbial communities, whilst soil pH had a major effect, by far the largest amongst the investigated parameters. Bacterial diversity was highest in neutral soils and minimal in acidic soils. Extremes of pH are also well documented to impose major constraints on root growth due primarily to the toxicities of ions such as Al^{3+}, Mn^{2+} and H^+ in the acidic range (Marschner 1995; Kinraide and Yermiyahu 2007), or HCO_3^- in the alkaline range (Tang et al. 1993). Additional effects are related to nutrient deficiencies such as that of iron in calcareous soils (Lemanceau et al. 2009) or phosphate in both acidic and alkaline soils (Richardson et al. 2009). Interestingly, through their physiological functions, plant roots and soil microbes are however capable of considerably altering soil pH relative to the bulk soil. Rhizosphere pH has been reported to be up to 1–2 pH units below or above bulk soil pH as shown in microcosms (e.g. Riley and Barber 1971; Gahoonia et al. 1992) or less frequently in situ (e.g. Yang et al. 1996; Michaud et al. 2007). This may have a dramatic effect on soil biogeochemistry, microbial communities

(including at the microsite scale, e.g. Strong et al. 1997) and may ultimately feed back on plant physiology or symbiosis (e.g. Cheng et al. 2004).

The pO_2 and hence the redox potential is highly variable in soils, with values which range from atmospheric pO_2 in the most aerobic conditions down to zero in strictly anaerobic conditions. These changes sometimes occur locally along short distances (Rappoldt and Crawford 1999), e.g. within small soil aggregates (Renault and Stengel 1994) as an effect of water content which affects the gas exchanges in the air-filled porosity, and largely as a result of biologically-mediated processes of O_2 consumption (Brune et al. 2000; Khalil et al. 2004; Pidello and Jocteur Monrozier 2006). As stressed by Brune et al (2000), the availability of O_2 has a major impact not only on the redox potential of the environment and many biogeochemical cycles, but also on the energetic situation of microorganisms. This is illustrated for nitrification/denitrification processes that rely on different bacterial communities which function either at high/low soil pO_2 (Focht 1992; Khalil et al. 2004). In addition, most plant species are highly sensitive to hypoxia/anoxia, only a few of them being able to cope with prolonged periods of low pO_2 as occur in submerged soil conditions (Perata and Alpi 1993). This is the case for wetland plants especially which have evolved specific strategies to cope with hypoxic conditions that prevail in the environments in which they grow.

Underlying processes

A primary function of below-ground organisms which can substantially impact soil pH is respiration and the subsequent increase in pCO_2. Because of respiration, bulk soil pCO_2 is well-known to be much (ten to hundred-fold) higher than that of the atmosphere (360 $cm^3 \ m^{-3}$). Karberg et al. (2005) reported values ranging from 7,000 to 24,000 (up to 32,000 under elevated atmospheric pCO_2) $cm^3 \ m^{-3}$ in a forest soil. Given that roots and microbes are major contributors to soil respiration, it is expected that rhizosphere especially in the region behind the root tip should be a hot spot of elevated pCO_2 and decreased pO_2 as shown by Bidel et al. (2000). This is however little documented in soils except the few data published by Gollany et al. (1993), who measured pCO_2 values in the order of about 100,000 $cm^3 \ m^{-3}$ at 1–3mm from

roots. The same holds for pO_2 values, although it is widely accepted that respiration should result in a decrease in pO_2 in the rhizosphere, with a notable exception for wetland plants (see below). Bidel et al. (2000) measured pO_2 values along the roots of *Prunus persica* (L.) Batsch seedlings and clearly showed that these were much smaller in the meristematic region of the root as a consequence of intense metabolic activity and respiration. They showed indeed that O_2 consumption in this region of the root was positively correlated with root growth. Only about 5×10^{-14} mol O_2 s^{-1} were consumed when no growth of the root tip occurred, whereas the respiration rate reached values greater than 35×10^{-14} mol O_2 s^{-1} for active meristems. Bidel et al. (2000) also estimated the relative contribution of microbial respiration to the observed decrease in pO_2. The corresponding flux decreased abruptly from 10 to 1 nmol O_2 m^{-3} gel s^{-1} within the 300 μm surrounding the root surface near the apex. These figures were however obtained in agar media, which is known to be rather hypoxic, and thus mimic the situation of a poorly aerated soil. Fischer et al. (1989) reported a decrease in redox potential (shift of Eh from about 700 to less than 380 mV) when the root tip of soil-grown faba bean (*Vicia faba* L.) reached the microelectrode. This phenomenon was reverted (Eh went back to initial value) about one-day later, once the root tip had moved away from the microelectrode, confirming that respiration was especially large near the meristematic zone of the root (apex). In contrast with aerobic conditions which are little documented for changes in pO_2 values in the rhizosphere, the case of wetland plants growing in hypoxic (submerged) soils has been extensively studied. To ensure the respiration of their root cells, those plants have evolved aerenchyma which conducts O_2 from the shoots to the roots (Armstrong 1979). Leakage of O_2 from roots can result in a local build-up of pO_2 in the rhizosphere of wetlands plants (Flessa and Fischer 1992; Revsbech et al. 1999; Armstrong et al. 2000; Blossfeld and Gansert 2007), which has been especially studied for rice (*Oryza sativa* L.). Revsbech et al. (1999) reported for instance that pO_2 increased up to a fifth of atmospheric pO_2 at rice root surface, while being almost nil at distances greater than 0.4 mm from the root surface.
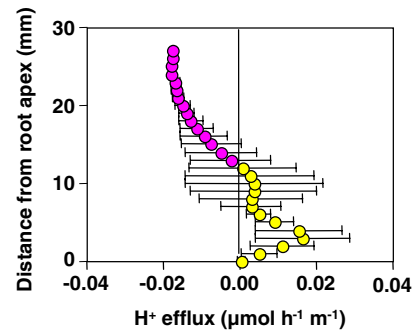
Given that CO_2 rapidly forms H_2CO_3 which is a weak acid (pK = 6.36), increased pCO_2 thus results in a decreased pH, in all but the most acidic soils (where

H_2CO_3 remains essentially undissociated). This actually means that in situ values for rhizosphere pH of calcareous soils are expected to be close to 7, rather than 8.3 as dictated by the dissolution/precipitation equilibrium of $CaCO_3$ at ambient pCO_2. For instance, based on the values measured by Gollany et al. (1993), Hinsinger et al. (2003) computed rhizosphere pH values of about 6.7–6.8. In spite of the current attention on aboveground pCO_2 it is rather astonishing that so little data is available about rhizosphere pCO_2 and its impact on belowground organisms and biogeochemical cycles. Greenway et al. (2006) have recently addressed this issue, especially the feedback effect of high pCO_2 on root growth, in the specific context of waterlogged soils where the excess of water impedes gas exchange and leads to elevated pCO_2 and low levels of pO_2.

In contrast, the major implications of proton influx/efflux from roots in rhizosphere pH changes have been studied in detail (see reviews by Nye 1981 and, more recently Hinsinger et al 2003). As elegantly shown by Marschner and co-workers with the use of dye indicators (Römheld and Marschner 1981; Marschner and Römheld 1983; Luster et al. 2009, Fig. 6), this process occurs in order to balance cation/anion net uptake (Raven 1986), and actually one should account for all charged compounds (ions) crossing the root cell membranes, e.g. organic anions (carboxylates) exuded by roots (Hinsinger et al. 2003). Net influx of excess cations results in a net efflux of protons and thus rhizosphere acidification, while alkalisation occurs for a net influx of excess anions over cations. Nitrogen which is in high demand by plants, has a major impact on this process as it is predominantly used as either an anion (nitrate) or a cation (ammonium), while it can be used as the uncharged species N_2 in symbiosis, such as in legumes. The former is expected to make the rhizosphere more alkaline, while the two latter forms of N acidify the rhizosphere (Riley and Barber 1971; Marschner and Römheld 1983; Le Bot et al. 1990; Gahoonia et al. 1992; Plassard et al. 1999; Tang et al. 2004). Rhizosphere alkalisation as related to proton influx confers an adaptative advantage for plant roots growing in acid soils by alleviating aluminium and other metal toxicities (Degenhardt et al. 1998; Pineros et al. 2005; Michaud et al. 2007). Rhizosphere acidification as related to proton efflux from roots is well known as an adaptative response of many plant

Fig. 6 Root-induced pH changes in Fe-deficient tobacco (*Nicotiana tabacum* L.). Roots were embedded in an agarose gel containing bromocresol purple as dye indicator to reveal the actual pH. The fluxes of protons as computed from the temporal change of pH are indicated to show that significant alkalisation (negative values of proton efflux) occurred along the basal portions of the roots, in contrast with the distinct apical acidification which was visible by the yellow color of the dye on the photograph (using the method described by Vansuyt et al. (2003). Reproduced by kind permission of Gérard Vansuyt, Gérard Souche and Benoît Jaillard)

species to iron and phosphorus deficiencies (Römheld and Marschner 1981; Tang et al. 2004; Lemanceau et al. 2009; Richardson et al. 2009).

Although many authors have been refering to the exudation of the so-called "organic acids" by roots (as reviewed by Jones 1998 and Ryan et al. 2001), it has been shown that carboxylates are dissociated at the cytosolic pH of root cells and thus exuded as anions. Their contribution to rhizosphere acidification thus largely depends on the previously-mentioned process, as stressed by Hinsinger et al. (2003). Beside roots, many soil microbes can produce organic acids and thus contribute to rhizosphere acidification as documented for ectomycorrhizal and saprophytic or pathogenic fungi massively producing oxalic acid (Dutton and Evans 1996; Wallander 2000; Casarin et al. 2004). Dramatic changes of pH can also occur as a consequence of the microbially-mediated oxidation of nitrogen (nitrification, e.g. Strong et al. 1997) or sulfur. Enhanced nitrification, which produces protons and nitrate ions with a stoechiometric 1:1 molar ratio, has been reported to occur in the rhizosphere relative to the bulk soil (Binnerup and

Sorensen 1992; Hojberg et al. 1996; Herman et al. 2006) and in wetland plants such as rice (Kirk and Kronzucker 2005). In such plants, the intimate coupling of rhizosphere pH changes with redox processes has also been documented for the case of iron oxidation and subsequent iron oxide precipitation. Begg et al (1994) and Kirk and Le Van Du (1997) calculated that this process resulted in a major proportion of the acidification measured in the rhizosphere of lowland rice, the other contributor being the use of ammonium as an important source of nitrogen under ambient reduced conditions, thus resulting in net proton efflux from rice roots. Neubauer et al. (2007) showed for *Juncus effusus* L. that this oxidation process was partly mediated by lithotrophic bacteria in the rhizosphere, besides oxygen leakage from root aerenchyma. Denitrification is another major process in the nitrogen cycle which is largely controlled by redox conditions. Pidello et al. (1993) showed that rhizosphere bacteria such as *Azospirillum brasilense* increased the soil redox potential, compared with the control (not inoculated) soil and consequently decreased by several-fold the

denitrifying activity of the soil. Pidello (2003) showed for another rhizosphere bacterium, *Pseudomonas fluorescens*, that strains varying in pyoverdine production affected the soil redox potential differently. Pyoverdines are strong, electro-active Fe chelators. Both strains of *P. fluorescens* decreased the soil redox potential, but the mutant strain that did not produce pyoverdine had a greater effect. The coupling of these processes implied in the biogeochemical cycling of Fe in the rhizosphere is further considered by Lemanceau et al. (2009).

Gradient, spatial and temporal heterogeneities

Soil pH, as many other chemical and physical properties, can substantially vary in space and time, as evidenced in both agricultural and forest ecosystems. Spatial variation is especially documented with changes over 0.5–3 units that are frequently reported within a small plot, a soil horizon and down to millimetric scales (Yang et al. 1995; Göttlein et al. 1996; Göttlein and Matzner 1997; Yanai et al. 2003; El Sebai et al. 2007). The spatial variability of pH buffering capacity is much less documented than pH heterogeneity, in spite of its functional relevance. Localised patches of organic matter or discrete distribution of $CaCO_3$ grains are likely to have a large influence on this parameter and on the subsequent changes of pH over time and space. One has to take into account this pre-existing heterogeneity of soil properties when investigating changes of pH in the rhizosphere in situ (in field-grown plants). This can be shown from the work of Schöttelndreier and Falkengren-Grerup (1999) who stressed that they could hardly distinguish between root-induced alteration of pH and utilisation of soil heterogeneity. Redox potential can also be subject to considerable variations in space and time, which are largely related to changes in soil water content, water saturation leading to decreases in pO_2 depending on the biological activities responsible for O_2 consumption and gas diffusivity. Besides the vertical gradient which is expected to occur in soils from the upper, aerated horizons down to deeper, water-saturated horizons, considerable heterogeneities can be observed at a much smaller scale within the soil matrix as shown when studying changes in redox potentials across small soil aggregates (Renault and Stengel 1994; Pidello and Jocteur Monrozier 2006).

Rhizosphere processes are obviously an additional source of heterogeneity (Hinsinger et al. 2005) and especially so for pH. These processes are driving forces for the formation of radial pH gradients around living roots. Evidence for such gradients which can extend up to several mm from roots has been reported by many authors (e.g. Schaller 1987; Gahoonia et al. 1992; Begg et al. 1994; Hinsinger and Gilkes 1996; Nichol and Silk 2001; Kopittke and Menzies 2004; Vetterlein and Jahn 2004b; Vetterlein et al. 2007b) since the early work of Farr et al. (1969) who showed a marked decrease in pH close to a root mat of onion (*Allium cepa* L.). With a refined root mat approach, Gahoonia et al. (1992) showed for ryegrass (*Lolium perenne* L.) that when fed with nitrate, the increase in pH reached about 1 pH unit while the decrease in pH amounted to 1.5 units when ammonium was supplied, the spatial extension of this phenomenon was about 2 mm in a luvisol and 4 mm in an oxisol. Recently Vetterlein and Jahn (2004b), Vetterlein et al. (2007b) and Bravin et al. (2008) have been studying the temporal development of similar gradients over time scales of several weeks, with a temporal resolution of several days, while Cornu et al. (2007) monitored pH changes in the rhizosphere with a daily resolution (but without studying the radial gradient in this case). Most of these studies have shown a more or less steady build-up of rhizosphere acidification or alkalisation over time. A finer temporal resolution would have been needed to account for the diurnal rhythm that one may expect, given that the uptake of ions and thus the resulting production/consumption of protons is known to follow diurnal rhythms as previously shown in hydroponically grown plants (Le Bot and Kirkby 1992; Rao et al. 2002; Tang et al. 2004), as well as the photosynthesis-driven diurnal patterns of exudation and thus of rhizosphere respiration. Most of the published work on pH gradients in the rhizosphere as described so far have however been obtained with root mat techniques which only give access to the average effect of many roots. This lead to an overestimation of the extent of the process compared with normal rhizosphere geometry and does not account for heterogeneities of pH along the root system of a single plant (Jaillard et al. 2003; Hinsinger et al. 2005). Limited studies, based on the use of microelectrodes have shown local gradients of pH (e.g. Schaller 1987; Nichol and Silk 2001) that vary according to the location along the root axis. Häussling et al. (1985)

showed in situ that rhizosphere acidification (0.3 pH unit change) occurred only behind the root tip of 60-yr old spruce (*Picea abies* (L.) Karst.) tree roots, while alkalisation occurred at the apex and more basal parts of the roots (reaching up to 0.8 pH unit change at the apex) in an acidic soil (bulk pH 4.2).

Remarkable studies of the spatial heterogeneities of pH changes in the rhizosphere have been published based on the use of dye indicators as initially developed by Weisenseel et al. (1979) and made popular by Marschner/Römheld and co-workers. Römheld and Marschner (1981), Marschner and Römheld (1983) showed for instance the typical localised acidification that occurs behind the root tips as a response to Fe deficiency in plant species belonging to the Strategy I of Fe acquisition. Such strategy has been shown to occur in all plant species but grasses (i.e. graminaceous plant species, which belong to Strategy II, see below) and is defined by enhanced proton efflux combined with enhanced Fe-reductase activity occurring behind root tips when such plants are exposed to low Fe availability which typically occurs in calcareous soils (Marschner 1995; Robin et al. 2008). Using a pH dye indicator combined with image analysis according to the method developed by Jaillard et al. (1996), Vansuyt et al. (2003) measured the variation of proton efflux along the axis of roots of Fe-deficient tobacco (Fig. 6). They showed that slight alkalisation (proton influx) was occurring along the basal part of the root while acidification (proton efflux) occurred at the root apex (up to 5–15 mm from the tip, Fig. 6). Similarly, a few works have been showing that P deficiency was also resulting in enhanced acidification of the rhizosphere, although this was not always localised at the root tip as for Fe (Gregory and Hinsinger 1999; Hinsinger et al. 2003; Tang et al. 2004). Plassard et al. (1999) comparing this technique with the use of microelectrodes in hydroponically-grown plants to derive proton effluxes confirmed the heterogeneity of such fluxes along root axes, even for plants which were not exposed to Fe or P deficiency. The combined use of proton and ion-selective electrodes (for measuring e.g. ammonium, nitrate and potassium concentration gradients and the corresponding fluxes) confirmed whether these patterns of proton efflux along roots were largely related to patterns of influx of major nutrients such as N and K which also substantially vary along roots and according to the mycorhizal status of roots in ectomy-

corrhizae (Plassard et al. 2002; Hawkins et al. 2008). Plassard et al. (2002) showed that nitrate and potassium influxes in long roots of mycorrhizal pine (*Pinus pinaster* Soland *in* Ait.) were not significantly different from those of non mycorrhizal roots, suggesting that proton efflux would be unaffected as well. In contrast they showed that influxes of nitrate and potassium were mainly affected by the mycorrhizal status and species in short mycorrhizal roots. Contrary to the long roots, much higher nitrate than potassium influx was found to occur in those roots (Plassard et al. 2002), suggesting that alkalisation should occur in the rhizosphere of short, mycorrhizal roots while slight acidification was expected in the rhizosphere of non infected, long roots. This suggests that the rhizosphere pH can be extremely heterogeneous along the root system of ectomycorrhizal plants, as also shown at a broader scale for seedlings growing in soil-filled rhizotrons by Casarin et al. (2003). These authors showed that acidification occurred in the rhizosphere of ectomycorrhizal roots, compared with the non mycorrhizal plant. Rigou et al. (1995) had formerly shown with a dye indicator that for pine seedlings grown in agar gels the roots of mycorrhizal plants were exhibiting larger proton effluxes and thus rhizosphere acidification than roots of non mycorrhizal plants. However, most of the literature on localised pH changes in the rhizosphere has been using techniques where plants are grown in rather artificial conditions such as hydroponic solutions or agar gels. Such simplified media which are transparent and thus allow visual observation of heterogeneities in the rhizosphere have been also successfully used to visualize redox changes occurring in rice (Trolldenier 1988). Using an oxygen depleted fluid agar medium, combined with redox microelectrodes, Armstrong et al. (2000) measured pO_2 gradients with high spatial resolution (10 μm) across roots and the rhizosphere of a wetland plant (*Phragmites australis* L.). They showed that at the apex, pO_2 increased from 5,000 cm^3 m^{-3} at 2 mm from the root surface to about 100,000 cm^3 m^{-3} at the root suface (and slightly more in the root cortex). Interestingly they showed that a much sharper gradient of pO_2 or almost no leakage of O_2 occurred at more basal parts of the root, suggesting that root-induced rhizosphere oxidation was rather confined to the apical region of the roots. The use of microsensors of O_2 was successfully used in both agar media and

water-saturated soils to study the gradient of pO_2 in the rhizosphere of rice (Revsbech et al. 1999).

Only few attempts have been made to assess pH and redox potential changes in soil grown plants. Recently Blossfeld and Gansert (2007) made a major step forward by using a foliar optical pH sensor which provided access to spatial heterogeneities of pH over several tens of cm^2 around roots of plants grown in rhizotrons. In addition their technique was sensitive enough to show a distinct diurnal rhythm with a larger acidification occurring in day-time than at night (Fig. 7). Although applied so far only to a wetland plant species (*Juncus effusus* L.) growing under reduced soil conditions, this technique and the future development of other similar sensors are promising tools to further our understanding of actual pH

changes occurring in situ. Previously, assessment of the temporal and spatial heterogeneities of pH changes had been achieved with the use of arrays of microelectrodes (Fischer et al. 1989) or soil solution samplers designed by Göttlein et al. (1996). Other solution samplers such as rhizons also provided valuable, discrete information on pH changes in the rhizosphere but they proved unable to monitor short-term (less than daily) or short-distance changes along a root or radially from the root because of sampling a quite large volume of soil solution (Cornu et al. 2007; Bravin et al. 2008). The design of non-invasive techniques as the one developed by Blossfeld and Gansert (2007) is in this respect much more helpful and promising (Luster et al. 2009).

Fig. 7 Temporal development of root-induced pH changes in the rhizosphere of growing roots of *Juncus effusus* L. Snapshots were obtained at different times from day 1 (D1) to day 2 (D2), with illumination starting at 0800 (8 am) and ending at 2200 (10 pm) each day. The colours indicate different pH values (see legend at the bottom) as measured non-invasively by the planar pH optode. The crossing points of the grid (top left) indicate the positions of fibre-optic pH measurements. The digital photograph (bottom right) shows the investigated section of the planar optode at the end of the time series with two roots (labelled I and II) growing across the pH optode (taken from Blossfeld and Gansert (2007) with kind permission by Blackwell Publish. Ltd.)
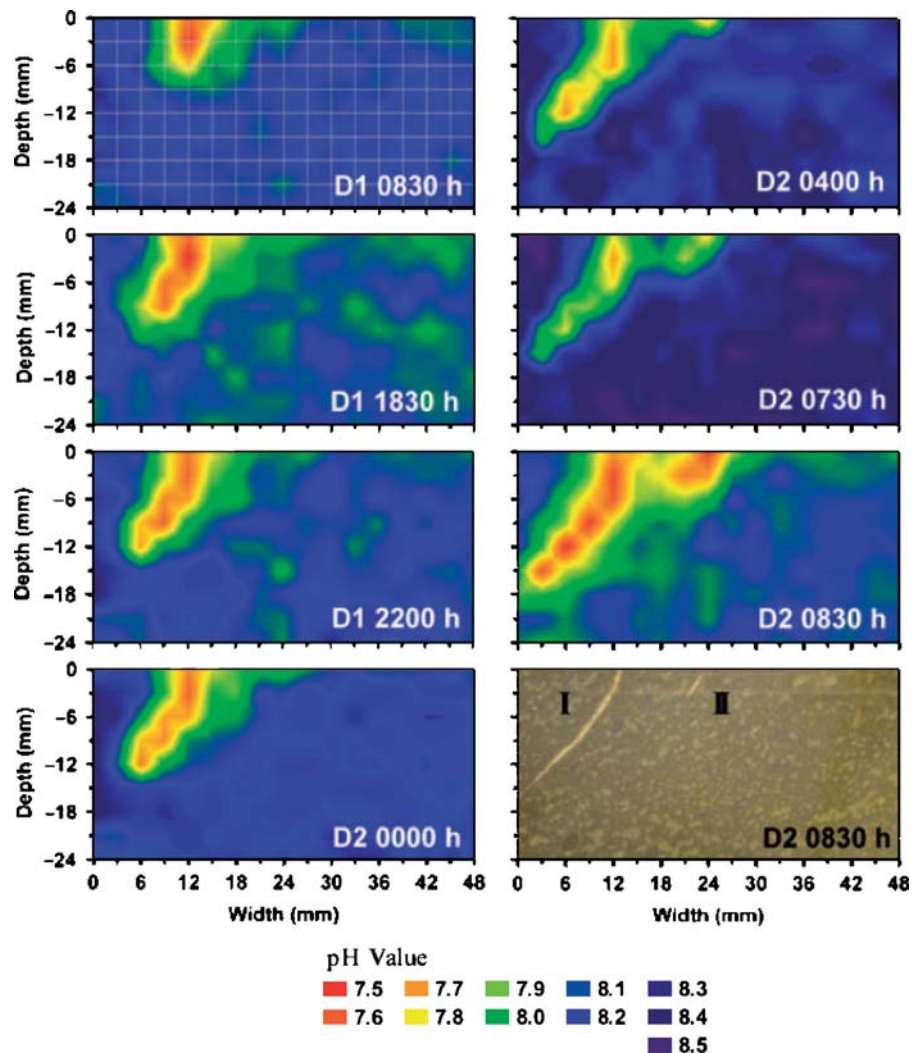
The pH buffering capacity of the soil is subject to considerable variations between soils and also possibly within a given soil as a function of the heterogeneities of distribution of constituents that play a key role in buffering the pH (e.g. particles or patches of organic matter or $CaCO_3$). As stressed by Hinsinger et al. (2003) based on the earlier work of Schubert et al. (1990) and Hinsinger and Gilkes (1996), little or no significant pH change may not mean the absence of proton fluxes in the rhizosphere, as these protons may be implied in a range of reactions that result in proton consumption (which make up the buffering capacity of the soil). These fluxes may have an important functional impact (e.g. on the subsequent mobilisation/immobilisation of nutrients) while pH changes would remain unaffected if the buffering capacity of the soil is large. This is illustrated in the work of Göttlein et al. (1999) who reported an increase in Al concentration close to growing roots (Fig. 8), in spite of an absence of significant pH change. Presumably, protons released by roots were consumed in reactions with the soil solid phase, e.g. exchange with Al-ions, which ultimately resulted in the observed increase in Al concentration. Beside its effect on the change in pH, the pH buffering capacity was found linearly correlated with the radial extension of pH gradients in the rhizosphere, as measured with microelectrodes around single roots (Schaller 1987).

The same holds for redox potential and may explain the reason why rhizosphere oxidation is often found to be confined to very short distances in water-saturated soils, typically less than a few hundred μm (Flessa and Fischer 1992; Revsbech et al. 1999; Bravin et al. 2008), possibly up to a few mm from the root surface (Begg et al. 1994; Armstrong et al. 2000). O_2 leaking from the roots is rapidly consumed in redox reactions such as the precipitation of iron oxides and a range of microbially-mediated processes (Revsbech et al. 1999; Bravin et al. 2008). Callaway and King (1996) have shown that, in addition to this, O_2 leaking from the roots of wetland plants such as *Typha latipholia* L. can be used by neighbouring plants (for respiration purposes) that would otherwise not withstand the low ambient pO_2. This was the evidence for O_2-mediated facilitation-competition taking place within this plant community.

In contrast with the spatial component of pH and Eh changes in the rhizosphere, the temporal component has been poorly documented, especially so over rather long terms (more than a few hours or days). Turpault et al. (2007) have been comparing in situ pH changes at two distinct seasons and have basically related the seasonal effect to the nitrification process and its link with cation/anion uptake balance. Investigating such long time scales requires in situ monitoring of pH, thus raising many methodological challenges, and the question of the location of the probes/sampling devices given the dynamic nature of root growth and development. Mathematical models are additional tools to solve these interdependent, complex temporal/spatial patterns as nicely shown over shorter scales by Kim et al. (1999) and Peters (2004). Kim et al. (1999) modeled the temporal evolution over a few hours up to 2 days of the axial and radial patterns of pH around a growing root tip, taking account of the growth of the root during this period of time. It should be stressed that efflux of protons also feeds back on root elongation (via cell-wall loosening) according to the acid growth theory, which further justify the necessity for coupling these two processes (Peters 2004). For redox potential, a few studies have been monitoring temporal changes of Eh over time. Cornu et al. (2007) and Bravin et al. (2008) have been monitoring redox potential close to a root mat (rhizobox approaches) with a daily resolution, in aerobic and anaerobic conditions, respectively. Continuous monitoring was achieved by Fischer et al. (1989) who could thereby relate the observed change of redox potential to the growth of the root of faba bean (*Vicia faba* L.). They showed that the decrease in Eh was fast (300 mV within about 1h) when the root apex approached the microelectrode. Then it slowly increased to reach its initial value after about 24 h (at a stage where the apex had grown a few mm further away), suggesting that such reduction was probably related to intense respiration in the meristematic zone of the root (apex). The combined pH-O_2 sensor foils developed recently by Blossfeld and Gansert (2007) shall provide a unique opportunity to map and monitor pH and redox potential changes in the rhizosphere of soil-grown plants over fine spatial and temporal resolutions, as shown for pH in the wetland plant *Juncus effusus* L. (Fig. 7). So far this has only been applied to ambient, reducing conditions and it would thus be very helpful to apply a similar technique for studying the spatial and temporal changes of redox conditions in plants growing in aerobic soil conditions.

Fig. 8 Temporal changes of Ca and Al concentrations, and Ca/Al ratios in the rhizosphere of growing roots of an oak (*Quercus ruber* L.) seedling. Soil solution was sampled at 3-week intervals with an array of microsuction cups positioned along a grid in a rhizotron, and analyses were performed with capillary electrophoresis (taken from Göttlein et al. (1999) with kind permission by Springer)
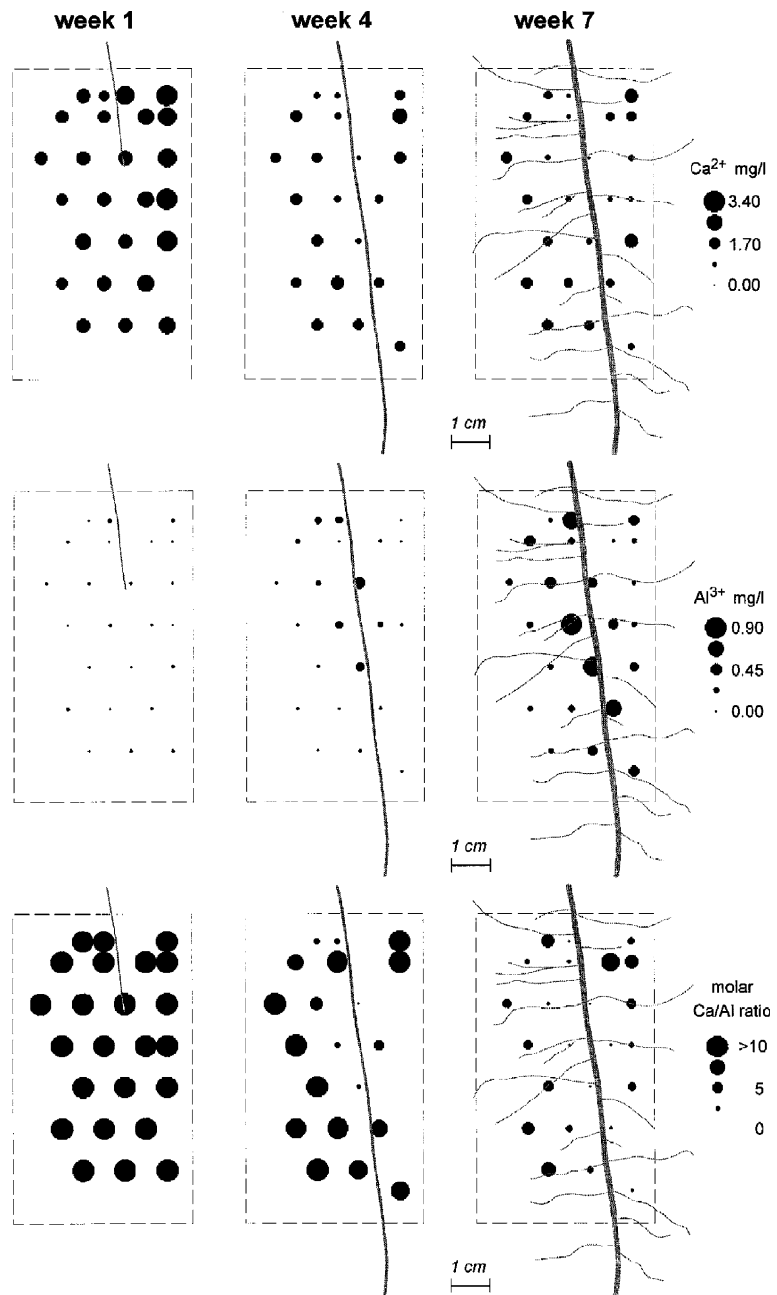
Nutrient distribution and accessibility in the rhizosphere

Ecological relevance

Compared with aquatic environments, soil environments are harsher because many nutrients are present in only small concentrations in the soil solution, being largely bound to the solid phase constituents. Their spatial distribution is far more heterogeneous than in aquatic environments and thus the spatial component of the bioavailability (accessibility) of nutrients is crucial. Plants and soil microorganisms have only limited ability to move towards nutrient-enriched zones, compared with animals. To cope with those conditions they have therefore evolved a whole range of strategies for accessing nutrient resources in the soil (Marschner 1995; Lambers et al. 1998; Richardson

et al 2009). Many of the underlying processes play a key role in nutrient cycling in soils (Kandeler et al. 2002; Philippot et al. 2009). Plants may create positive feedbacks to nutrient cycling because of species' differences in carbon deposition and competition with microbes for nutrients in the rhizosphere. Plant species' effects can be as or more important than abiotic factors, such as climate, in controlling ecosystem fertility (Hobbie 1992). The availability of organic matter is a major driver for heterotrophic microorganisms, and plants play a considerable role through either litter deposition or rhizodeposition in the rhizosphere (Jones et al 2004, 2009; Wardle et al. 2004).

The scarcity of many nutrients in soils also means that harsh competition occurs for these nutrients and ultimately determines the structure of microbial communities, as evidenced for iron and phosphorus. The most nutrient-efficient microorganisms are thereby efficiently selected in the rhizosphere (Marschner et al. 2006; Calvaruso et al. 2007; Robin et al. 2008; Lemanceau et al 2009). Such competition also occurs between plant roots of neighbouring species and may ultimately drive the composition of plant communities (e.g. Callaway et al. 2002; Raynaud et al. 2008). In alpine and arctic soils where the availability of inorganic nitrogen is especially low due to slow rates of organic matter mineralisation, plant communities are dominated by those species that can make use of amino-acids or ammonium rather than nitrate (Chapin et al 1993; Raab et al. 1996; Lambers et al. 1998). Modelling diffusion of nutrients in the rhizosphere of neighbouring roots proved an efficient approach to further understanding some of the key processes involved in plant-plant interactions. Craine et al. (2005) showed for instance that higher nitrate uptake capacity (I_{max}) of one plant species led to larger depletion zones around its roots and thus played a central role in pre-empting nitrate and out-competing less efficient roots of neighbour plants. Raynaud et al. (2008) further refined this model by accounting also for the diffusion of exudates, showing that large diffusion rates of root exudates may result in increased bioavailability of nutrients such as phosphate for neighbouring plant roots which do not exhibit same exudation potential, thereby contributing to facilitation rather than competition.

The occurrence of nitrogen-fixing legumes also plays a major role in structuring plant and microbial communities as a result of the build-up of nitrogen availability in soils (Spehn et al. 2000). This means that besides competition for nutrients, facilitation and complementarity are other major driving forces of ecosystem productivity (Callaway and Walker 1997; Callaway et al. 2002; Gross et al. 2007). This is obvious for mutualistic relationships between the host plant and the microsymbiont in mycorrhizal or rhizobial associations. However, there is an increasing interest for understanding how it operates between plant species living in communities (Callaway and Walker 1997; Callaway et al. 2002), either in grassland or agroforestry and other intercropping systems (Paynel and Cliquet 2003; Gross et al. 2007; Li et al. 2007; Li et al. 2008).

Underlying processes

Rhizodeposition is a primary process altering nutrient abundance in the rhizosphere. The corresponding flow of carbon results in a local build-up in C-rich substrates that fuel the growth of heterotrophic microbial communities (Lynch and Whipps 1990; Nguyen 2003; Jones et al. 2004, 2009). The rhizosphere thus appears as enriched soil microsites, along with other hotspots of microbial activities such as plant debris and dead bodies (detritusphere). While the bulk soil is C-limiting for microbial growth (Wardle 1992), the rhizosphere is rather N-limiting than C-limiting. A priming effect can occur in the rhizosphere leading to enhanced decomposition of soil organic matter, as reviewed by Kuzyakov (2002) who stressed that reduced decomposition could sometimes occur as well. Such priming effect is the consequence of rhizodeposition and especially so root exudation releasing simple substrates with low C:N ratios, stimulating rhizosphere microorganisms to decompose soil organic matter to meet their N requirements. Rhizosphere enrichment in inorganic N is however unlikely to occur due to microbes and plants competing for the acquisition of the released N, as recently modelled by Raynaud et al. (2006) who also accounted for the exudation of N-rich compounds such as amino-acids. The fate of C and N is further complicated in the rhizosphere if one accounts for the whole microbial loop including predators such as protozoae and nematodes (Bonkowski 2004; Bonkowski et al. 2009).

Nutrient transfer via mass-flow and diffusion occurs in the rhizosphere because of water and

nutrient uptake by roots, and is another major driving force of nutrient redistribution in the rhizosphere. Nutrients that occur as solutes in the soil solution are transferred via mass-flow towards the root surface when the plant is transpiring. Nutrients that are abundant in the soil solution may thereby accumulate in the rhizosphere whenever their flow exceeds plant's demand. This typically occurs for Ca and Mg, and has been also reported to occur for K (Lorenz et al. 1994; Barber 1995; Clegg and Gobran 1997; Vetterlein and Jahn 2004b; Turpault et al. 2005). Precipitation of gypsum (Ca sulfate, Fig. 9) and calcite (Ca carbonate) have been reported to occur as a consequence of the build-up of Ca concentration in the rhizosphere (Hinsinger 1998). In contrast, when the flow of nutrient transferred via mass-flow is less than plant's requirement, their concentration decreases in the rhizosphere (Lorenz et al. 1994; Barber 1995; Jungk 2002; Hinsinger 2004). Such depletion typically occurs for P and micronutrients, as well as for N and K in many cases, and generates a diffusion gradient towards the root surface (Hendriks et al. 1981; Kuchenbuch and Jungk 1982; Gahoonia et al. 1992; Ge et al. 2000; Jungk 2002; Hinsinger et al. 2005). The rhizosphere can thereby appear as a nutrient-enriched or -impoverished zone.

Besides the above-mentioned physical processes, roots and rhizosphere microorganisms can also alter the nutrient concentration via a range of chemical and biochemical processes (Darrah 1993; Hinsinger

1998; Hinsinger et al. 2005). Changes of pH in the rhizosphere can for instance dramatically influence the availability of nutrients via competition of protons for metal cations on cation exchange sites (e.g. for Cu and Zn; Loosemore et al. 2004; Michaud et al. 2007) or via shifting the dissolution/precipitation equilibria of nutrient-bearing minerals as shown for e.g. Mg (Hinsinger et al. 1993; Calvaruso et al. 2006) and P (Gahoonia et al., 1992; Begg et al. 1994; Hinsinger and Gilkes 1996; Bertrand et al. 1999; George et al. 2002a). In addition, exudation of organic ligands by roots and rhizosphere microorganisms may further increase the availability of nutrients via either ligand exchange-promoted desorption of anions (e.g. phosphate-ions desorbed by mucilage or carboxylates: Geelhoed et al. 1999; Hinsinger 2001; Ryan et al. 2001; Read et al. 2003; Dunbabin et al. 2006) and/or complexation of metal cations, as documented for carboxylates (citrate or oxalate) and siderophores of microbial or plant origin. These can thereby promote the dissolution of metal-bearing minerals as shown for Ca and Fe (Jones and Darrah 1994; Wallander 2000; Casarin et al. 2004; Reichard et al. 2005, 2007) and/or increase the total concentration of metal cations in the soil solution (Gerke et al. 2000; Reichard et al. 2005, 2007). In submerged soils where ambient anoxic conditions prevail and lead to excess (toxicity) of metal nutrients such as Fe and Mn (occurring as reduced species), their concentration can be decreased in the rhizosphere of wetland plants and rice as a
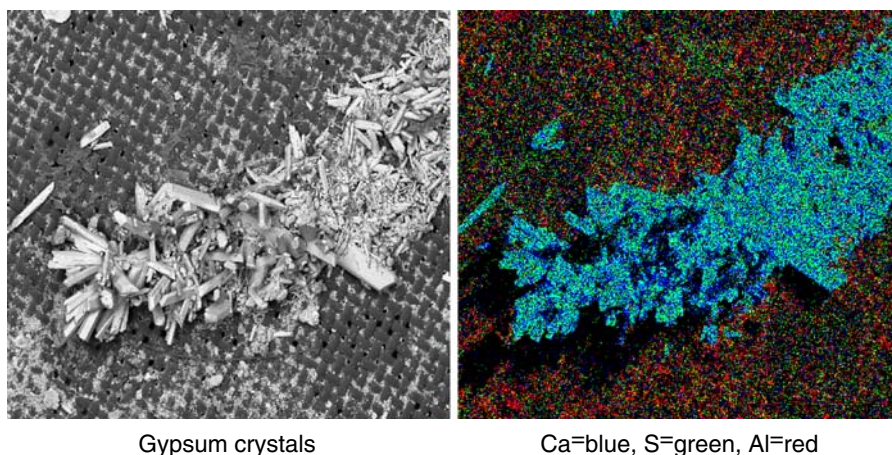

Gypsum crystals

Ca=blue, S=green, Al=red

Fig. 9 Crystals of gypsum (Ca sulfate) precipitating close to a root of pine (*Pinus sylvestris* L.) growing along a 30 µm nylon mesh (on the other side of the mesh) in a rhizobox experiment. The micrograph (left box) was obtained with a scanning electron microscope, while the corresponding elemental maps (right box) were obtained by EDX analyses (Reproduced by kind permission of Doris Vetterlein)

consequence of redox reactions and Fe plaque formation (Begg et al. 1994; Bravin et al. 2008). Besides playing a major role in root- and microbe-mediated Fe cycling in the rhizosphere (Neubauer et al. 2007), this Fe plaque can sequester other nutrients such as phosphate and zinc (Kirk and Bajita 1995; Saleque and Kirk 1995). Another major process that can concur to altering the availability of nutrients in the rhizosphere is the release by roots and micro-organisms of enzymes implied in the hydrolysis of organic forms of nutrients such as N, P and S, as documented extensively for phosphatases (George et al. 2002b, 2004 and 2006; Kandeler et al. 2002; Li et al. 2004; Denton et al. 2006; Richardson et al. 2009).

The concurrence of the various above-mentioned processes can lead to both enrichment and impover-ishment of nutrients in the rhizosphere as shown for instance for P (Fig. 10). A given fraction of soil P can be depleted close to roots and accumulate at further distance from roots as shown by Hübel and Beck (1993) or Hinsinger and Gilkes (1996). It has been more frequently reported that some P fractions are depleted while others are increased in the rhizosphere, with neat differences between plant species (Geelhoed et al. 1999; George et al. 2002a; Li et al. 2008). What is little known is the quantitative contribution of the various above-mentioned processes to the actual pattern of nutrient distribution observed in the rhizosphere, even more so when different species live in a community. Modelling can help unravel these processes (Raynaud et al. 2008). Most of the few investigations on the rhizosphere of soil-grown plants have reported greater nutrient concentrations than in bulk soil (Courchesne and Gobran 1997; Schöttelndreier and Falkengren-Grerup 1999; Pankhurst et al. 2002; Turpault et al. 2005). However, as stressed by Schöttelndreier and Falkengren-Grerup (1999) and Hinsinger et al. (2005), it is difficult to distinguish between actual rhizosphere enrichment or preferential colonization of nutrient-rich patches or root macropores in such studies. This is a clear limitation of in situ experiments as the nutrient foraging behavior has been shown as an important strategy for nutrient acquisition in higher plants (Leyser and Fitter 1998; Robinson et al. 1999; Hodge 2004; Hodge et al. 2009) including ectomycorrhizal (roots and hyphae) plants (Read and Perez-Moreno 2003; Rosling et al. 2004). Root architecture matters more for the more poorly mobile nutrient P than for relatively mobile N, but conversely the plasticity of
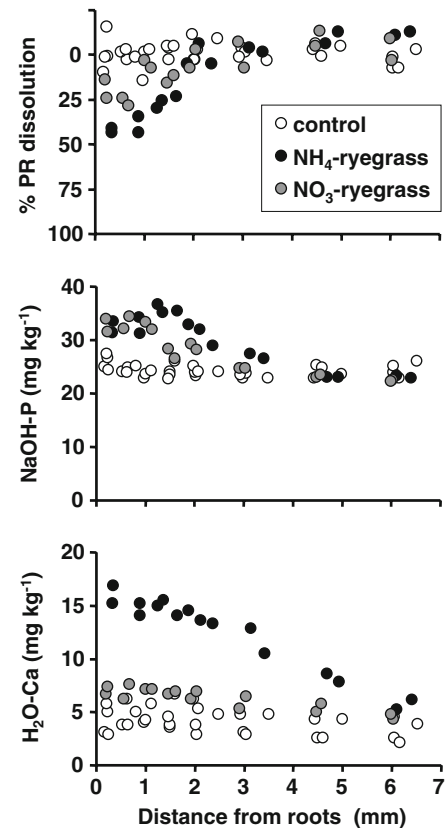

Fig. 10 Gradients of P and Ca in the rhizosphere of ryegrass (*Lolium rigidum* L.) supplied with a phosphate rock (PR) as sole source of P and Ca, and with N as either nitrate only (NO_3) or nitrate and ammonium (NH_4), relative to control treatment without plant. The extent of the dissolution of PR was deduced from the measurement of total Ca and was greater when ammonium was supplied as a consequence of greater root-induced acidification. Part of the dissolved P and Ca (resulting from PR dissolution) which were not taken up by ryegrass accumulated in the rhizosphere and were recovered in the alkali-soluble and water-soluble fractions respectively, over varying distances and extents, depending on N source (taken from Hinsinger and Gilkes (1996) with kind permission by Blackwell Publish. Ltd.)

root systems has been shown to be greater for patchy distribution of N than P (Fitter et al. 2002; Linkohr et al. 2002).

Gradients, spatial and temporal heterogeneities

Distribution of nutrients is far from uniform in soils, and roots are an additional source of heterogeneity, which builds up over time in the rhizosphere, along the course of root growth. This was shown for instance by Göttlein et al. (1999) for Ca in an acidic

forest soil (Fig. 8). As for water, nutrient uptake is not uniform along a growing root (Clarkson 1991). Even if environmental conditions like water content, temperature, and root soil contact are homogeneous, there is a distinct pattern of uptake for specific nutrients as shown in nutrient solution by Harrison-Murray and Clarkson (1973) and Ferguson and Clarkson (1975). They clearly showed that Ca uptake was much larger at the root tip that in older regions of the root because of the suberised endodermis restricting the radial flow of those nutrients which preferentially use the apoplastic pathway. In their studies, other nutrients which are known to use the symplasmic pathway of radial flow towards the root stele, such as P and K, were evenly taken up along the root length. For nutrients other than Ca and Mg, contradictory results can be found in the literature. For maize roots highest phosphate uptake was found for 1-day old root zones and uptake declines to 25 to 30% in 26-day old zones (Ernst et al. 1989). This uptake pattern was likely related to the presence and life span of root hairs. A similar pattern of uptake was observed for nitrate by Reidenbach and Horst (1997) who suggested that such differences in uptake should be reflected in uptake models by forming root age classes with different uptake rates. Reidenbach and Horst (1997) also observed a marked diurnal variation in uptake, which was larger at lower light intensity. Diurnal patterns of exudation which derive from the change of availability of photosynthates in the plant as shown for instance for citrate release by proteoid roots (Keerthisinghe et al. 1998, Dessureault-Rompré et al. 2007) are also possibly implied in a diurnal pattern of P acquisition. In this respect, the most remarkable circadian pattern is that described for phytosiderophore release in iron deficient graminaceous plant species (Walter et al. 1995; Reichman and Parker 2007). A distinct peak of secretion occurs between 3 and 6 h after the onset of light, which is quite a more efficient strategy for efficient Fe acquisition than evenly releasing such ligands at a lower flux all day long (Robin et al. 2008). Focussing their secretion in a narrow temporal and spatial (it is occurring at greater flux behind the apex) window minimises the risk of being metabolised by rhizosphere microorganisms prior to chelating Fe (Darrah 1991). Specialized organs such as ectomycorrhizal roots and cluster roots are additional sources of heterogeneities in exudation, uptake and acquisition of nutrients along root systems (Plassard et al. 2002;

Casarin et al. 2003; Shane and Lambers 2005; Lambers et al. 2006).

Radial gradients of nutrients around roots due to depletion or accumulation can extend over less than 1 mm up to several cm depending on their mobility in the soil (Fig. 10). Depletion of P, K and nitrate typically occurs over about 1, 5 and more than 10 mm for these ions, respectively (e.g. Jungk and Claassen 1986; Darrah 1993; Jungk 2002; Hinsinger 2004). For phosphate, the least mobile of major nutrients, the radial gradient which normally does not extend more than about 1 mm can be increased up to about 2 mm by root hairs (Gahoonia et al. 2001; Ma et al. 2001). If plants are mycorrhizal, the hyphae can extend even further into the soil and resulting in a depletion of P over several mm (Li et al. 1991). Although, little documented, reverse gradients can occur for nutrients such as Ca which tend to accumulate in the rhizosphere as a consequence of mass-flow exceeding the actual uptake flux into the root (Fig. 10).

Water uptake, nutrient uptake, exudation of protons and release of organic acids or enzymes, are processes that are likely to have a different temporal and spatial pattern. Nutrient gradients in the rhizosphere, which results from the interplay of all these processes and transport processes (mass flow and diffusion), can thus considerably vary in both space and time. At a spatial point of view, in a few cases, complex concentration profiles have been shown to occur for nutrients such as P (Fig. 10), as a consequence of the combination of an uptake-driven depletion gradient and a soil P mobilisation-driven accumulation gradient, the latter being the consequence of the exudation of protons (Hinsinger and Gilkes 1996), carboxylates (Kirk 1999) or possibly phosphatase enzymes (Hübel and Beck 1993). This means that nutrient uptake and transport processes (of the considered nutrient only) as accounted for in most models derived from that of Nye and Marriott (1969) only explain a portion of the observed gradients for nutrients such as P. Indeed, one should also account for the gradients of protons (Gahoonia et al. 1992; Hinsinger and Gilkes 1996) and exudates (George et al. 2002b) that may contribute to further mobilisation/immobilisation of P in the rhizosphere, as well as phosphatases of both root and microbial origins (Tarafdar and Jungk 1987; Chen et al. 2002; George et al. 2002b; Kandeler et al. 2002). Those exudates that are more mobile (e.g. protons

rather than enzymes) are thus likely more efficient at providing extra nutrients to the root (Hinsinger et al. 2005). For instance, the poor mobility of enzymes in the soil (due to strong adsorption onto soil particles) is likely to explain the poor performance for P acquisition of transgenic plants transformed to secrete a phytase of fungal origin relative to control plants once grown in soils, while the difference was considerable in soil-free media (George et al. 2004 and 2005).

Such complex interplay of processes is dynamic. For example as K requirement is high for young plants but decreases with age, K depletion at the root surface can be observed in young plants (12 days old) while accumulation was found for older plants (29 days old) by Vetterlein and Jahn (2004b). Accumulation of easily available K in the rhizosphere as recorded in situ for field-grown plants such as forest trees can also result from the combination of uptake-driven depletion and weathering of K-bearing minerals or organic matter which over longer time scales may contribute a net increase in soil solution and exchange-able K in the rhizosphere (Clegg and Gobran 1997; Turpault et al. 2005). If studies are conducted in soil and not in hydroponics, care should be taken in interpreting soil solution concentrations. Soil solu-tion concentrations may increase/decrease due to transport exceeding/falling short of plant uptake or mobilisation/immobilisation reactions. However, changes in soil solution concentrations can also be a consequence of changes in the amount of solute, i.e. soil water content (Vetterlein and Jahn 2004b). Typically, soil water content/soil matric potential rapidly decreases at the root surface compared with the bulk soil (see above). Thus increased soil solution concentrations at the root surface may just reflect decreases in soil water content. The same is true for chemical substances released from the roots like organic anions, protons or enzymes. The amount released dissolves in a smaller volume of water and their diffusion into the bulk soil is hindered as diffusion coefficients decrease with decreasing water content.

Temporal dynamics of nutrient gradients, neglect-ing additional water content gradients, are illustrated by Kirk (2002) and Geelhoed et al. (1999) for P. In their model calculations these authors predicted soil solution P concentration profiles with increasing distance from the root surface. In both models, the release of citrate by roots and citrate degradation with

time and interaction with P adsorbed on surfaces or P in mineral phases were taken into account as well as citrate diffusion away from the root surface. Both models predict, for certain time intervals, a strong increase in soil solution P concentration close to the root surface and a decrease within the first millimetre from the root surface. With time the steepness of gradients decreases. These predictions are in close agreement with experimental data based on soil solution sampling over time (Vetterlein et al. 2007b).

Kirk's and Geelhoed's models, in contrast to earlier models of Nye and Marriott (1969) or Claassen et al. (1986), already take into account the interaction of a number of chemical species. Kirk's approach (Kirk 2002) is basically an extension of that proposed by Nye (1983) to account for the interaction of two solutes diffusing in opposite directions (e.g. phos-phate and a root exudate) via an interaction term. It can hardly be generalised as it cannot account for the more complex situation of P biogeochemistry and biochemistry in the rhizosphere, where solution P concentration results from many more than two counteracting processes (mass-flow and diffusion of P-ions and exudation of diverse exudates being possibly interacting). The approach developed by Geelhoed et al. (1999) is more mechanistic but applies to a simplistic situation where only one type of solid constituent (goethite) interacts via a single mechanism (adsorption/desorption) while in practice P concentrations also depend on a range of dissolution/ precipitation equilibria and organic P hydrolysis in the rhizosphere (Hinsinger 2001; Hinsinger et al. 2005). Only sophisticated geochemical models or ideally models that couple numerous, biogeochemical reac-tions and transport processes can account for such complex rhizosphere chemistry (Anoua et al. 1997; Nowack et al. 2006). This type of approach which takes into account the chemical speciation in soil solution was recently extended by Szegedi et al. (2008) by the development of the RhizoMath model. It is based on coupling the mathematical package MATLAB with the geochemical code PHREEQC. RhizoMath's greatest advantage is that different geochemical models (with and without charge bal-ance) and geometries (planar and radial) are already included. Moreover, due to its graphical user interface the tool can be applied without changing the source code or a complex input file. RhizoMath can be used as a tool to integrate processes occurring simulta-

neously in the rhizosphere and it has the potential to function as a submodule for larger scale plant growth models to build in rhizosphere processes.

Conclusions

Life on planet Earth is sustained by a small volume of soil surrounding roots and influenced by living roots, called the rhizosphere. This micro-environment concentrates much of Earth's biodiversity, being probably the most dynamic habitat on Earth (Jones and Hinsinger 2008). As it represents the interface between soils and plants, the rhizosphere plays a key role in defining the quality and quantity of the Human terrestrial food resource on the one hand, and on soil formation on the other hand, via the input of organic carbon deep in the substratum. Despite its central importance to all life below and aboveground, we know very little about the intimate functioning of the rhizosphere, and even less about how best we can manipulate it to our advantage. We especially lack a holistic perception of the rhizosphere and have an extraordinary ignorance of the intimate connections between the biology, physics and chemistry of the system, which thereby exhibits astonishing spatial and temporal heterogeneities. Whilst important insights have been made by individual disciplines, we postulate that the next great advances will be through interdisciplinary approaches that implicitly account for biophysical and biogeochemical processes, driven by a range of theoretical frameworks designed to predict important functions such as water uptake, food production and soil sustainability.

The rhizosphere exhibits a unique biophysics and biogeochemistry which contrasts from that of the bulk soil, thereby explaining the diversity of habitats it harbours for microorganisms. Besides determining those microbial habitats, the inner physical structure is the basis for describing movement and storage of elements and water as well as the ability of roots to explore the soil. This ultimately determines the accessibility of water and nutrients to the roots and associated microorganisms, as well as the biogeochemical environment, via the partial pressures of O_2 and CO_2, and thereby the redox potential and pH of the rhizosphere, respectively. We urgently need to improve our methodology to describe this physical architecture at the micro scale and to express these findings not only

in a descriptive manner but to interpret the data in respect to their functional relevance.

Noninvasive methods may be the tool to improve knowledge on the physical architecture and may in addition provide new insights into spatial and temporal dynamics of porosity, soil strength and water distribution around single roots. Unfortunately these methods still face a trade-off between spatial resolution and field of view and different methods are optimum for obtaining detailed information on structure (e.g. X-ray), water (e.g. neutron radiography) and roots (e.g. microscopy). Non-invasive methods for visualising the distribution of elements in situ with a similar spatial resolution are unfortunately not available at present. Two-dimensional developments as exemplified by the optode foil for the measurement of temporal changes of pH, redox potential and pCO_2 are however opening up new opportunities. While much progress has been made recently for exploring the spatial dimension of rhizosphere processes, our knowledge of their temporal dimension is still scarce. In addition, as stressed by Watt et al. (2006a), the paucity of reliable data obtained under field conditions underlines the rudimentary state of our knowledge of root-microorganism interactions in real world conditions.

With improvements in spatial and temporal resolution of measurements the need for models to integrate this information increases as the different parameters interact with each other and show different dynamics in space and time. There are promising approaches under way that allow new modules to be added as knowledge increases. There remains the challenge of integrating such detailed models into root growth and root architecture models for upscaling of rhizosphere processes (Standing et al. 2007). This last step is crucial to reflect rhizosphere processes in field, regional or global scale models. Our knowledge of the rhizosphere biophysics and biogeochemistry has been increasing tremendously during the last few decades, opening possible new applications to a range of major ecosystem services at a much broader scale than the soil/root/microorganism interface. Major progress will be achieved if scientists are able to bridge the micro- and macro-scales, from the rhizosphere of individual roots to soils at field scales and larger.

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