Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective

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Abstract Soils are the product of the activities of plants, which supply organic matter and play a pivotal role in weathering rocks and minerals. Many plant species have a distinct ecological amplitude that shows restriction to specific soil types. In the numerous interactions between plants and soil, microorganisms also play a key role. Here we review the existing literature on interactions between plants, microorganisms and soils, and include considerations of evolutionary time scales, where possible. Some of these interactions involve intricate systems of communication, which in the case of symbioses such as the arbuscular mycorrhizal symbiosis are several hundreds of millions years old; others involve the release of exudates from roots, and other products of rhizodeposition that are used as substrates for soil microorganisms. The possible reasons for the survival value of this loss of carbon over tens or hundreds of millions of years of evolution of higher plants are discussed, taking a cost-benefit approach. Co-evolution of plants and rhizosphere microorganisms is discussed, in the light of known ecological interactions between various partners in terrestrial ecosystems. Finally, the role of higher plants, especially deep-rooted plants and associated microorganisms in the weathering of rocks and minerals, ultimately contributing to pedogenesis, is addressed. We show that rhizosphere processes in the long run are central to biogeochemical cycles, soil formation and Earth history. Major anticipated discoveries will enhance our basic understanding and allow applications of new knowledge to deal with nutrient deficiencies, pests and diseases, and the challenges of increasing global food production and agroecosystem productivity in an environmentally responsible manner.

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Introduction

Most plants depend on soil, but plants and their associated microorganisms also play a crucial role in the formation or modification of soil (Pate et al. 2001; Pate and Verboom 2009; Taylor et al. 2009). Soil results from the weathering of rocks and minerals, and can have various properties according to the origin of the parent material, climate and vegetation. Soil C is predominantly derived from plants, directly or indirectly, and whilst weathering may be due to physical and chemical influences, most weathering processes involve plants, primarily roots, or microbial activities that depend on root-derived C (Raven and Edwards 2001; Beerling and Berner 2005; Taylor et al. 2009).

The focus of this review is on the long-term, evolutionary dimension of the interactions between plant roots, microorganisms and soil in the rhizosphere. We discuss their consequences for the development of terrestrial ecosystems, the functional diversity of the plant and microbial communities, biogeochemical cycles and soil formation. These interactions require communication between numerous organisms involved in rhizosphere processes. In recent years, much has been learned about these interactions, and how organisms have coevolved. We also discuss how different processes involved in plant-soil interactions dominate at different stages of primary or secondary succession.
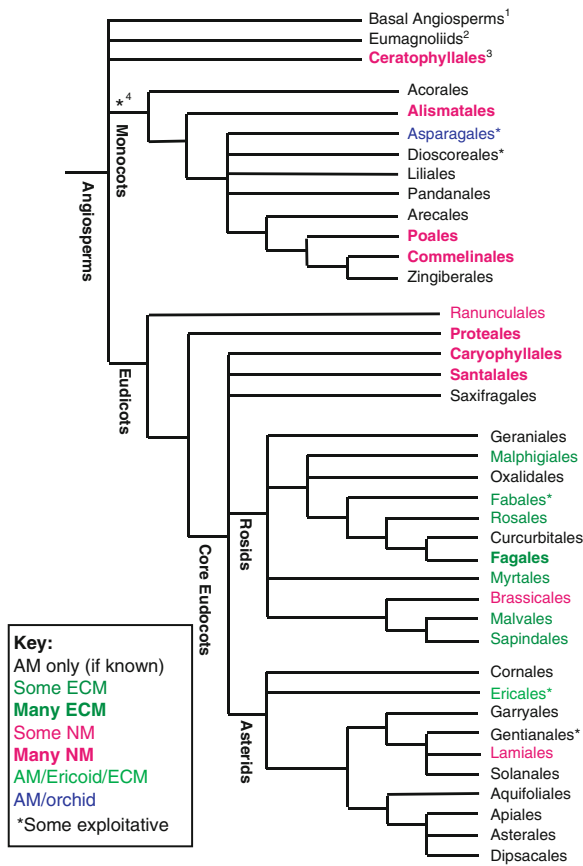
We present a selection of major ecosystem processes that occur in the rhizosphere, but then focus on a limited number of examples in an evolutionary context, given the scarcity of information that is available in the literature. Inevitably, a substantial part of our knowledge on long-term evolutionary processes is based on information on contemporary processes, and hence the discussion on the evolutionary context remains rather speculative.

Nutrient acquisition

Next to water and temperature, nutrients are the environmental factor that most strongly constrains terrestrial plant growth. The productivity of virtually all natural ecosystems, even arid ecosystems, responds to addition of one or more nutrients, indicating widespread nutrient limitation. Mineral nutrients such as P or Fe are very reactive and strongly bound to soil particles. Their availability is generally low, especially in calcareous soils. Plant species differ greatly in their capacity to acquire nutrients from soil. Some plants are capable of acquiring Fe, P or other ions from calcareous soils, whereas others cannot extract enough nutrients to persist on such soils (Lambers et al. 2008b). Nutrient acquisition from calcareous soils involves rhizosphere processes, such as the exudation of phosphate-mobilising carboxylates (Hinsinger 2001) or the release of Fe-chelating phytosiderophores (Römheld 1987; Ma et al. 2003; Robin et al. 2008). Phytosiderophores also mobilise other micronutrients whose availability at high pH is low, e.g., Zn (Römheld 1991; Cakmak et al. 1996, and Cu (Chaignon et al. 2002; Michaud et al. 2008).

Phosphate acquisition from soils with low P concentrations in solution as well as plant growth can be enhanced by mycorrhizal symbioses (Bolan 1991; Richardson et al. 2009). However, even when P acquisition or plant growth are not enhanced in the presence of mycorrhizal fungi, the P taken up by the fungus may represent a major fraction of the total amount of P acquired by the mycorrhizal plant (Smith et al. 2003). Approximately 80% of all higher plant species can form a mycorrhizal symbiosis; of these, the arbuscular mycorrhizal (AM) association is the most common (Brundrett 2009) (Fig. 1), especially on relatively young soils (Lambers et al. 2008a). AM is also the most ancient among mycorrhizal symbioses (Table 1), the first evidence dating back to more than 400 million years ago (Remy et al. 19994; Brundrett 2002). On somewhat older soils, AM are partly replaced by ectomycorrhizas and ericoid mycorrhizas, which are considered more advanced and diverse mycorrhizal symbioses (Brundrett 2002); the latter symbioses are capable of accessing forms of both P and N (Leake and Read 1989; Cairney and Burke 1998) that are not available for AM fungi (Bolan et al. 1987; Yao et al. 2001). Mycorrhizal associations are frequently beneficial for both symbiotic partners (Table 1). Plants benefit from the fungi because these acquire nutrients, which are inaccessible for the plant because of distance from the roots, location in pores that are too small for roots to access, or, occasionally, occurrence as forms that are unavailable to plants. Conversely, fungi ensure a supply of C derived from photosynthesis by the plant (Smith and Read 2008). On extremely poor soils, when virtually all P is

Basal Angiosperms[1]
Eumagnoliids[2]
Ceratophyllales[3]
Acorales
Alismatales
Asparagales*
Dioscoreales*
Liliales
Pandanales
Arecales
Poales
Commelinales
Zingiberales
Ranunculales
Proteales
Caryophyllales
Santalales
Saxifragales
Geraniales
Malpighiales
Oxalidales
Fabales*
Rosales
Curcurbitales
Fagales
Myrtales
Brassicales
Malvales
Sapindales
Cornales
Ericales*
Garryales
Gentianales*
Lamiales
Solanales
Aquifoliales
Apiales
Asterales
Dipsacales

*[4]
Monocots
Angiosperms
Eudicots
Core Eudicots
Rosids
Asterids

Key:
AM only (if known)
Some ECM
Many ECM
Some NM
Many NM
AM/Ericoid/ECM
AM/orchid
*Some exploitative

Fig. 1 Phylogenetic position of mycorrhizal lineages in a simplified Angiosperm family tree, with indications of the extent of the mycorrhizal status within each plant family (modified after Brundrett 2002, with kind permission of Blackwell Science Ltd.)

strongly sorbed onto soil particles, the 'scavenging' strategy of mycorrhizas is not effective (Parfitt 1979). On such soils, which are common in old landscapes, species with root clusters that release a range of exudates that effectively 'mine' P are prominent (Lambers et al. 2006, 2008a) (Fig. 2). Many species that produce root clusters (Fig. 3) are non-mycorrhizal, but some are capable of associating with mycorrhizal fungi as well as making clusters (Reddell et al. 1997; Lambers et al. 2006). On strongly acidic or alkaline soils, where P is bound to Al and Fe or Ca complexes, respectively, the mining strategy would also be effective. Indeed, many actinorhizal species and Cyperaceae with root clusters are common in acidic bogs (e.g., Crocker and Schwintzer 1993; Skene et al. 2000) or on calcareous dunes (e.g., Oremus and Otten 1981; Bakker et al. 2005). However, no systematic studies have focused on the

role of root clusters in these environments, and further research is warranted.

The non-mycorrhizal habit of many cluster-bearing plant species (Shane and Lambers 2005b) presents an intriguing situation from an evolutionary perspective, because ancestors of these non-mycorrhizal species were most likely all arbuscular mycorrhizal (Brundrett 2002). We know that some of the non-mycorrhizal families with root clusters, e.g., Proteaceae, are as old as early- to mid-Tertiary (Hopper and Gioia 2004), but there is no information about the time these lineages became non-mycorrhizal. Brundrett (2002) provided evidence for the view that the evolution of specialised strategies of nutrient acquisition, such as cluster roots and also new types of mycorrhizas, coincided with the origin of numerous plant families, which thereby became more competitive, especially so in certain nutrient-limited habitats. Such nutrient-acquisition mechanisms may have provided a selective advantage to those plant lineages in which these new strategies evolved, resulting in increased nutrient acquisition, albeit presumably at increased C costs.

Brundrett (2009) pointed out that cost/benefit analyses are rather complex to make, given that mycorrhizal plants remain dominant in most habitats, while a major group of non-mycorrhizal plant species is found in marginal environments, especially extremely infertile soils in the case of cluster-bearing species (Lambers et al. 2008a). Non-mycorrhizal species also occur in waterlogged, saline, dry, metal-contaminated, or cold habitats where plant productivity is low and inoculum of mycorrhizal fungi could be scarce (Brundrett 2002). Interestingly, at least one species in the Proteaceae is mycorrhizal as well as cluster-bearing, i.e. *Hakea verrucosa*, which is endemic on ultramaphic soils, which have high Ni concentrations (Boulet and Lambers 2005). The AM habit of a species endemic on soil rich in Ni and belonging to a typically non-mycorrhizal family is not unique for Proteaceae. The grassland community of a California serpentine soil includes two species from non-mycorrhizal families, *Arenaria douglasii* (Caryophyllaceae) and *Streptanthus glandulosus* (Brassicaceae) (Hopkins 1987). Boulet and Lambers (2005) speculate that massive release of carboxylic acids would mobilise not only phosphate, but also Ni, rendering this toxic for root growth. Indeed, root growth, in particular cluster-root growth, of *H. verrucosa* is at least as sensitive to Ni in nutrient

Table 1 Estimated age, evolutionary and functional categories of plant-fungus associations (after Brundrett 2002)

	Pathogen	Endophyte	AM	ECM	Ericoid	Orchid	Exploited
Association:							
Estimated age of association (million years)	> 1000	> 400	> 400	> 100	< 100	+/−100	recent
Plant provides a key habitat for fungus	+	+	+	+ / −	− ?	?	− ?
Fungus efficient at mineral nutrient acquisition from soil	−	−	+	+	+	+	− or +
Interface hyphae highly specialised	+	−	+	+	−	−	+ or −
Plant-fungus coevolution	−	−	+	+	?	−?	−
Host-fungus specificity	varies	high?	low	medium	medium	high, medium	extremely high
Ecological role:							
Mineral nutrient transfer to plant	−	−	+	+	+ ?	+	+
Energy transfer to fungus	+	+ / −	+	+	+ ?	− or + ?	−
Energy transfer to plant	−	−	− (+)	− (+)	−	+ or −	+
Plant:							
Switched to new fungus lineages			−	+	+	+	+
Recruitment of new plant lineages continues	+	+	?	+	−	−	+
Photosynthesis	+	+	+ (−)	+ (−)	+	+ (−)	−
Obligate requirement for association	−	−	+ or +/−	+	+?	+ or −	+
Fungus:							
Multiple lineages of fungi	+	+	−	+	+	+	+
Recruitment of new fungal lineages continues	+	+	−	+	+?	+	+
Obligate (host required for growth)	+	+ or − ?	+	+	?	−	−
Capable of independent growth (in axenic culture)	+ or −	+	−	+ or −	+	+	+ or −

Question marks indicate uncertain roles where further investigation is required, while brackets indicate unusual states that occasionally occur

solution as is the root growth of the congeneric *H. prostrata* (F.M. Boulet and H. Lambers, unpubl.). Given that Proteaceae, Caryophyllaceae and Brassicaceae are typically non-mycorrhizal, the AM habit of *H. verrucosa*, *A. douglasii* and *S. glandulosus* has probably evolved fairly recently, from non-mycorrhizal ancestors, but nothing is known about the time or nature of such events.

There is at least one species in the Proteaceae that is mycorrhizal without cluster roots, i.e. *Placospermum coriaceum* from the rainforest in north-eastern Australia (P. Reddell, V. Gordon and M. Webb, pers. comm.). In comparison with Proteaceae from the same rainforests (*Darlingtonia darlingiana*, *Carnarvonia* sp. and *Musgravea heterophylla*), *Placospermum coriaceum* produces relatively little dry weight at very low total soil P concentrations (< 25 mg P kg^{-1} soil), but performs similarly or better at higher P concentrations (>50 mg P kg^{-1} soil), when *Musgra-*

vea heterophylla suffers from P toxicity (P. Reddell, V. Gordon and M. Webb, pers. comm.). Species in the genus *Persoonia* (Proteaceae) produce neither root clusters (Purnell 1960) nor mycorrhizas (Brundrett and Abbott 1991). This is puzzling, as *Persoonia* species occur on severely P-impoverished soils, suggesting an alternative root adaptation, which has yet to be discovered. Again, we can only speculate about the mycorrhizal status of the ancestors of *Persoonia* species.

Nitrogen acquisition can be enhanced greatly by symbiotic N_2 fixation, which is common in legumes, with the exception of species belonging to the less-specialised subfamily Caesalpinioideae (Vessey et al. 2005). The fact that nodulation is uncommon in this subfamily, more common in Mimosoideae and very common in Papilionoideae is in line with the idea that the three legume subfamilies evolved in the order Caesalpinioideae, Mimosoideae and Papilionoideae.
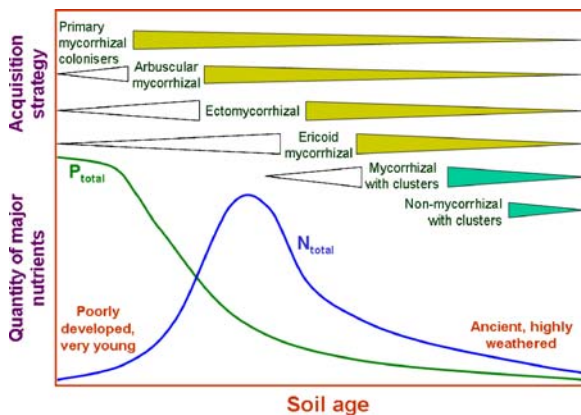
Fig. 2 Changes in total soil P and total N as a function of soil age and in plant nutrient-acquisition strategies (modified after Lambers et al. 2008a). The soil age scale spans from 'poorly developed, very young soils' (which stands for soils resulting from recent volcanic eruptions) to 'ancient, weathered soils' (i.e. soils that have been above sea level and have not been rejuvenated by glaciations over several millions of years). Some mycorrhizal species may co-occur with non-mycorrhizal cluster-bearing species in severely P-impoverished soils, but they never become dominant. The width of the triangles referring to the different ecological strategies of nutrient acquisition provides a (relative) measure of the abundance of these strategies as dependent on soil age. The total P levels in soils range from 30 to 800 mg kg^{-1}, while N levels range from <5 to 8000 mg kg^{-1}

However, as pointed out by Sprent (2007), recent results suggest that Caesalpinioideae and Papilionoideae appeared about 60 million years ago, early in the Tertiary, while Mimosoideae evolved 20 million years later. It has been hypothesised that nodulation evolved about 55 million years ago, i.e. at a time when the atmospheric CO_2 concentration had increased substantially. Nitrogen thus likely became limiting for plant growth, favouring the process of N_2 fixation, which occurs at the expense of the total C fixed by the host plant (Sprent 2007; Sprent and James 2007). Legumes form root nodules with rhizobia (Franche et al. 2009). Actinorhizal species (e.g., *Alnus*, *Casuarina*, *Myrica*) form symbiotic N_2-fixing nodules (rhizothamnia) with Actinobacteria, and cycads (e.g., *Ceratozamia*, *Macrozamia*) form N_2-fixing structures (coralloid roots) with cyanobacteria (Vessey et al. 2005; Franche et al. 2009). Outside the plant families mentioned above, symbiotic N_2 fixation is extremely rare. Symbiotic N_2 fixation is particularly important during primary succession on young soils with very low soil N levels (Walker and Syers 1976; Crews et al. 1995) as well as during secondary succession after

a fire, when a large fraction of N in biomass has been volatilised (Halliday and Pate 1976). During primary or secondary succession, soil N levels steadily increase, and the ecosystem changes from predominantly N limited to being limited increasingly by P (Parfitt et al. 2005; Lambers et al. 2008a).

Some ericoid mycorrhizas and ectomycorrhizas (ECM) belonging to groups that are incapable of symbiotic N_2 fixation may access complex organic N, including peptides and proteins (Högberg 1990). Some may even access very poorly accessible N that is locked up in protein-tannin complexes (Read 1996; Read and Perez-Moreno 2003). This capacity to access protein-tannin complexes is not universal, however (Bending and Read 1996). For the ECM
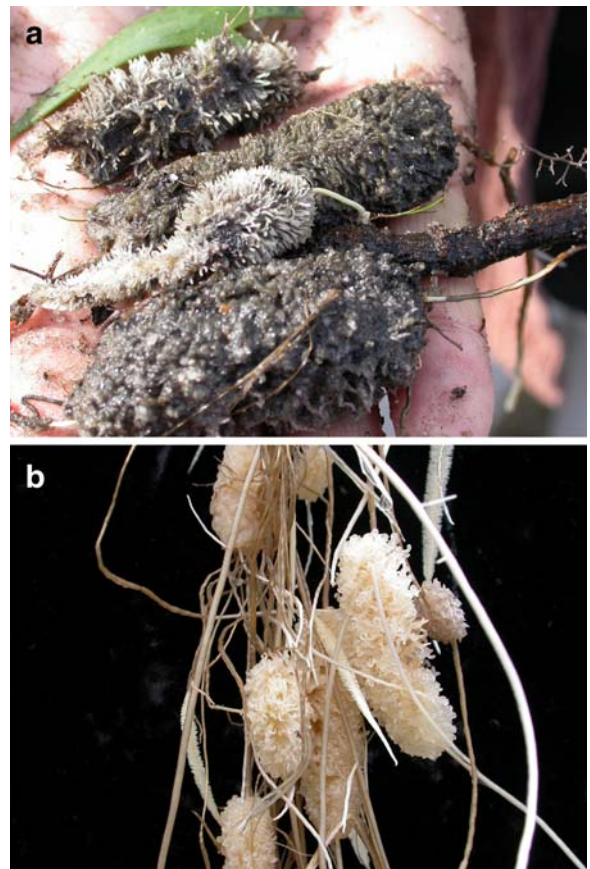
Fig. 3 Root morphology of Australian Proteaceae. Clusters of *Hakea ceratophylla*, freshly dug up in Alyson Baird reserve, Perth, Western Australia (**a**); clusters of *Hakea prostrata* plants grown in nutrient solution (**b**). Photos courtesy of Michael W. Shane (School of Plant Biology, the University of Western Australia)

association of red pine (*Pinus resinosa*) and *Pisolithus tinctorius,* N uptake into red pine occurs only in the presence of saprotrophic microorganisms (Wu et al. 2003).

Symbiotic microorganisms can obviously play a key role in accessing complex organic N, bypassing saprotrophs involved in mineralisation. However, in some mycorrhizal systems these saprotrophs play a pivotal role in making N available to the plants. The AM fungi also increase N nutrition by extending the absorptive zone due to hyphal extensions (Jonsson et al. 2001; Lerat et al. 2003) described as the 'mycorrhizosphere'. This increase in N uptake is related to the stimulation of bacteria grazing in the rhizosphere.

Predator-prey interactions in the rhizosphere are an important aspect to stimulate plant growth according to the 'microbial loop in soil'; this mechanism involves protozoa and nematodes (Clarholm 1985; Bonkowski 2004; Bonkowski et al. 2009). These interactions have recently been modelled by Raynaud et al. (2006). An increase in microbial density in the rhizosphere stimulates bacterial grazers such as protozoa. Grazing of bacteria contributes to excretion of one third of the ingested N as ammonia (Zwart et al. 1994). Ammonia contributes to plant growth directly or after its transformation by nitrifying soil microorganisms, which provide nitrate to the plant (Bonkowski et al. 2001).

The presence of protozoa decreases the length of fungal hyphae by 18%, while the presence of ectomycorrhizas leads to a reduction in numbers of bacterial and protozoan grazers (38% and 34%, respectively) (Bonkowski et al. 2001). These results point to a significant trade-off in C allocation between bacterial and fungal communities in the rhizosphere due to mutualistic root symbionts that act as a sink for C (Vance and Heichel 1991; Bago et al. 2000; Johnson et al. 2002). Despite this conflict in C allocation, a synergistic microbial effect enhances uptake of N (17%) and P (55%) in the combined association of mycorrhizas and protozoa where hyphal networks increase N uptake due to protozoa-mobilised N (Bonkowski et al. 2001). Symbiotic N_2 fixation is typically very important in young landscapes and during secondary succession, as discussed above; conversely, the role of mycorrhizas capable of accessing complex nitrogenous compounds, including protein-tannin complexes tends to become more important on older soils (Lambers et al. 2008a).

Molecular communication

Communication in the rhizosphere is pivotal for many interactions and their corresponding evolution. Several molecular signalling pathways, particularly in bacteria, have been well characterised, highlighting the ability of bacteria to 'sense' plant-derived compounds. Bacteria are also able to modulate plant functioning by producing phytohormone-like molecules. In addition, severe competition between microorganisms in the rhizosphere involves specific communication between microorganisms, including quorum-sensing and complex mechanisms that modulate it (Faure et al. 2009). Symbiotic associations as discussed above require intricate signalling between the macrosymbiont (host plant) and the microsymbionts (guest microorganisms). This signalling is best understood for the legume-rhizobium symbiosis, where flavonoids and betaines are released by legume roots (Vessey et al. 2005; Franche et al. 2009). However, other signalling molecules are also involved in the legume-rhizobium interactions that lead to a symbiosis (Faure et al. 2009). The signalling molecules released from roots bind with a bacterial gene product, and then interact with a specific promoter in the genome of rhizobium. This promoter is associated with the genes responsible for inducing nodulation (the nodulation, or *nod* genes). The products of these genes (Nod factors) induce root-hair curling on the plant and cortical cell divisions, which are among the earliest, microscopically observable events in the nodulation of most legume species. When rhizobia adhere to root hairs, the cell wall of the affected root hair is partly hydrolysed at the tip, allowing the bacteria to enter. An infection thread is formed by invagination of the cell wall (Gage and Margolin 2000). Alternatively, rhizobia may enter through cracks in the epidermis, associated with lateral-root formation, or wounds (Sprent 2007). However, also in that event, effective signalling must occur for a nodule to emerge.

The actinorhizal symbiosis between plant species like *Alnus glutinosa* and the Actinobacteria *Frankia* also involves the release of specific compounds (flavonols) that enhance the level of nodulation, but their exact role in the process is yet unknown (Van Ghelue et al. 1997, Vessey et al. 2005). Very little is known about the chemical nature of attractants from hosts to cyanobacteria (Vessey et al. 2005).

Major progress is being made on signalling between roots and AM fungi, highlighting the importance of strigolactones (Akiyama et al. 2005, Paszkowski 2006). Strigolactones are a group of sesquiterpene lactones, previously isolated as seed-germination stimulants for some parasitic weeds (Yoneyama et al. 2008). Strigolactones induce extensive hyphal branching in germinating spores of the AM fungus *Gigaspora margarita* at very low concentrations (Bouwmeester et al. 2007). In AM plants, strigolactone release is greatly enhanced under phosphate starvation (López-Ráez et al. 2008; Yoneyama et al. 2008). Isolation and identification of plant symbiotic signals open up new ways for studying the molecular basis of plant-AM fungus interactions. This discovery also provides a clear answer to a long-standing question on the evolutionary origin of the release from host roots of signalling molecules that stimulate seed germination in parasitic plants (Akiyama and Hayashi 2006). Signalling between host and fungus also plays a role in mycorrhizal associations other than AM, but we know much less about this (Martin et al. 2001).

Plants not only communicate via the release of root exudates with symbiotic microorganisms and parasitic higher plants, but also with roots of neighbouring plants (Bais et al. 2004). Some of the released exudates have positive effects, e.g., Fe-mobilising phytosiderophores and phosphate-mobilising carboxylates, as discussed above. These positive effects may lead to *facilitation*, i.e. amelioration of the environment of neighbouring plants (Lambers et al. 2008b), as recently modelled by Raynaud et al. (2008). Other exudates have a negative effect on growth of neighbours. If the roots of the neighbouring plants are of a different species, these effects are called *allelopathic*; if the roots are of plants of the same species or even the same plant, the effects are called *autotoxic* (Lambers et al. 2008b).

Allelopathy or interference competition is hard to demonstrate in nature. One of the more convincing studies was done on *Centaurea maculosa*, a Eurasian species that has become an invasive weed in North America (Ridenour and Callaway 2001). Using activated carbon, which adsorbs allelochemicals, it can be demonstrated that the allelochemical released from the roots of *C. maculosa*, (±)-catechin, inhibits root growth of neighbouring grasses such as *Festuca idahoensis*. Somewhat surprisingly, (±)-catechin con-

centrations in bulk soil are rarely very high, suggesting that the effect of (±)-catechin is exhibited only when roots are in close proximity and casting doubt on the claim that this allelochemical accounts for the invasive nature of *C. maculosa* (Perry et al. 2007). Some species, e.g., *Lupinus sericeus* and *Gaillardia grandiflora*, are resistant to (±)-catechin, because they exude increased amounts of oxalate upon exposure to (±)-catechin. Oxalate blocks (±)-catechin-triggered generation of reactive oxygen species and thus reduces oxidative damage (Weir et al. 2006). Another allelochemical (3,4,5-trihydroxybenzoic acid or gallic acid) that gives rise to the formation of elevated levels of reactive oxygen species in roots of neighbouring plants is released by another invasive weed, *Phragmites australis*. Gallic acid leads to acute rhizotoxicity. Unlike (±)-catechin, gallic acid is persistent in *P. australis*'s rhizosphere (Rudrappa et al. 2007).

Autotoxicity can lead to soil sickness, i.e. gradual declines in crop yield in the absence of crop rotations (Lambers et al. 2008b). It is quite common in cucurbit crops, e.g., *Citrullus lanatus*, *Cucumis melo* and *C. sativus* (Yu et al. 2000). Cinnamic acid is one of the autotoxic compounds involved; again, it induces formation of reactive oxygen species (Ding et al. 2007). Autotoxicity may also be involved in responding to obstructions in soil. Semchenko et al. (2008) found that grass species characteristic of nutrient-poor habitats restrict placement of their root mass in substrate containing obstructions. This response disappears in the presence of activated carbon, indicating the effect of inhibitory chemicals.

Upon attack of roots of *Thuja occidentalis* by larvae of *Otiorhynchus sulcatus* (a weevil), these roots release chemicals and thus attract *Heterorhabditis megidis*, a parasitic nematode, which preys on the weevil larvae (Van Tol et al. 2001). Similar below-ground tritrophic interactions occur in *Zea mays*. Upon attack by beetle larvae, their roots release a sesquiterpene, (E)-β-caryophyllene, which attracts entomopathogenic nematodes and increases the effectiveness of these nematodes in finding and killing herbivore larvae (Rasmann et al. 2005; Turlings and Ton 2006). Our rapidly increasing knowledge of below-ground tritrophic interactions is expected to provide opportunities for applications in plant management systems, similar to those existing for above-ground tritrophic interactions (Turlings and Wäckers 2004). From an evolutionary point of view, little is

known, however, about when such complex interactions first appeared.

Rhizodeposition

Rhizodeposition is the release of C compounds from living plant roots into the surrounding soil; it is a ubiquitous phenomenon (Jones et al. 2004, 2009). The loss of C from root epidermal and cortical cells leads to a proliferation of microorganisms inside (endophytes), on the surface and outside the root. Rhizodeposition results in different chemical, physical and biological characteristics in the rhizosphere compared with those of the bulk soil. The magnitude of these changes is determined by the amount and type of C released from the root, as well as intrinsic soil characteristics. Rhizodeposition basically results from two different processes: (1) leakage of compounds over which the plant exerts little control; (2) exudation of specific compounds with a specific function and over which the plant exerts control (Jones 1998). Leakage of compounds as defined here represents a minor component of a plant's C budget, less than 5% of all C daily fixed in photosynthesis (Lambers et al. 2008b). Higher values cited in the literature probably include C released by either root respiration or from dying root cells (Lambers 1987). Jones et al. (2009) provide quantitative data derived from meta-analyses of published datasets in their recent review.

Plant roots may release massive amounts of organic compounds via rhizodeposition

Rates of exudation *sensu stricto* vary widely among species and environmental conditions. At neutral pH and optimum P supply, rates tend to be low. In Al-resistant species, carboxylate-exudation rates tend to increase at low pH, in the presence of Al (Kochian et al. 2005). Dependent on species, the predominant carboxylates are malate (Delhaize et al. 1993) or citrate (Miyasaka et al. 1991), and in a few plant species, oxalate (Zheng et al. 1998). Cultivars of rice (*Oryza sativa*) that are resistant to Pb release oxalate when exposed to Pb (Yang et al. 2000). Similarly, roots of *Triticum aestivum* release malate and citrate when exposed to Cu (Clemens et al. 2002). The role of the released carboxylates is to chelate Al and other

metals, and thus prevent harmful effects of the toxic metal, when occurring as free metal cationic species.

Iron-efficient grasses release phytosiderophores when their growth is limited by the availability of Fe (Ma 2005; Robin et al. 2008). The phytosiderophores are released from the root tips only (Marschner et al. 1987), predominantly during the early morning (Takagi et al. 1984; Ma and Nomoto 1994). Robin et al. (2008) stress that this is an efficient strategy to maximise the positive impact on Fe acquisition by minimising the breakdown of phytosiderophores by rhizosphere microorganisms, in agreement with model calculations of Darrah (1991). Neighbouring Fe-inefficient plants may benefit from these released phytosiderophores (facilitation), and this knowledge can be applied in intercropping Fe-efficient crops with calcifuge ones, e.g., maize (*Zea mays*) with peanuts (*Arachis hypogaea*) (Zuo et al. 2000) or red fescue (*Festuca rubra*) with fruit trees (Ma et al. 2003).

Many plants enhance their rate of carboxylate exudation when their P supply is severely limiting (Vance et al. 2003). Massive exudation rates are exhibited by species that produce root clusters at very low P supply (Watt and Evans 1999; Shane and Lambers 2005b). Root-cluster-bearing species, e.g., *Lupinus albus* (Fabaceae; Watt and Evans 1999), *Hakea prostrata* (Proteaceae; Shane et al. 2004) and *Schoenus unispiculatus* (Cyperaceae; Shane et al. 2006) release carboxylates in an exudative burst. This ensures mobilisation of P before microorganisms have an opportunity to decompose the released exudates, according to model calculations of Darrah (1991). Moreover, root clusters of *Lupinus albus* drastically reduce the cluster-root rhizosphere pH, thus inhibiting bacterial activity; they also release phenolics, which induce fungal sporulation, as well as chitinases and glucanases, which degrade fungal cell walls, prior to the exudative burst (Weisskopf et al. 2006). This complex strategy ensures minimal degradation and maximum efficiency of exuded carboxylates to mobilise scarcely available P and micronutrients.

Whilst rhizodeposition incurs a loss of C to the plant, there are obviously also major benefits. First, there is the signalling to microsymbionts, as discussed above; this only incurs a minor C cost. Second, exudation *sensu stricto* can have a major impact on nutrient acquisition. Phytosiderophores and other chelating agents play a pivotal role in acquiring Fe

and other micronutrients, especially from calcareous soil (Römheld 1987; Ma 2005; Robin et al. 2008). They incur a relatively small C cost, because release rates are relatively low and restricted in space (from root tips only) and time (in the early morning only) (Cakmak et al. 1996). Carbon costs associated with carboxylate release to chelate and detoxify Al or other metals are also relatively small, as only root tips appear to be involved in this process (Delhaize and Ryan 1995).

Carbon costs associated with carboxylate exudation to enhance P acquisition are substantial, since the carboxylates must be exuded in quantities sufficient to solubilise sorbed P (Lambers et al. 2006). Given that root clusters are short-lived, i.e. approx. three weeks in *Lupinus albus* (Watt and Evans 1999) and *Hakea prostrata* (Shane et al. 2004), and less than two weeks in *Schoenus unispiculatus* (Shane et al. 2006), this strategy is probably very costly in terms of C requirements. Solid data on the C costs of root clusters, including the costs of the carboxylates they release, are unavailable. Estimates of the costs of the production, respiration and carboxylate release of cluster roots of *Hakea prostrata* are as high as 50–100% of daily rates of photosynthesis. However, it should be borne in mind that *Hakea prostrata*, like other cluster-bearing plants in Mediterranean environments, produces root clusters only during the wet winter months, so that the C costs on an annual basis are probably four times less (Lambers et al. 2006).

The cost of rhizodeposition is balanced by benefits provided by microorganisms

Plants live in association with a rich diversity of microorganisms during their entire development. These associations correspond to a gradient of plant-microbe interactions from mutualism to parasitism, even in the case of symbionts such as mycorrhizal fungi (Johnson et al. 1997) (Fig. 4, Table 1). These interactions involve complex trophic relations between plants and soil microorganisms. These interactions, called the rhizosphere effect (Hartmann et al. 2008), correspond to the stimulation of microbial community activities in the rhizosphere compared with those in the bulk soil due to C released by roots, i.e. rhizodeposition.

Whilst some plants release exudates in such a way as to minimise rapid breakdown by microorganisms, as discussed above for root-cluster-bearing species and grasses releasing phytosiderophores, plants may
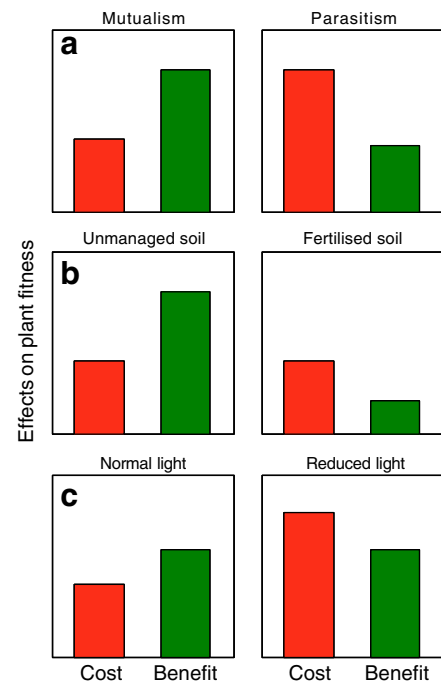
Fig. 4 Mycorrhizal associations can be either mutualistic, when the benefit of the association for the plant exceeds the cost, or parasitic when costs exceed benefits (**a**) (reproduced after Johnson et al. 1997, with kind permission from Blackwell Science Ltd.). The cost-benefit relationship varies with environmental conditions where the symbiosis occurs; upon fertilisation, the growth benefit of the mycorrhizal association decreases, and the cost may outweigh the benefit, ultimately leading to a parasitic association (**b**). Similarly, a low light intensity may increase the cost of photosynthate production above the benefit from the symbiotic association, thus also resulting in a parasitic association (**c**)

also stimulate the growth of rhizosphere organisms. Some of these microbial-growth promoting effects are clearly beneficial for plant growth, e.g., by acting as antagonists for deleterious microorganisms (Schippers et al. 1987; Raaijmakers et al. 2009), by releasing plant growth substances (Dobbelaere et al. 1999; Faure et al. 2009) or promoting non-symbiotic N_2-fixing microorganisms (Döbereiner and Pedrosa 1987; Saubidet et al. 2002; Richardson et al. 2009). However, the potential of associative N_2-fixing bacteria to promote the growth of cereals and grasses by enhancing the availability of combined N is generally limited. Positive effects of inoculation with these bacteria on plant growth are due to, e.g., synthesis of phytohormones and vitamins, and inhibition of plant ethylene synthesis (Richardson et al. 2009). These bacteria may also be able to decrease the

deleterious effects of pathogenic microorganisms, mostly through the synthesis of antibiotics and/or fungicidal compounds (Dobbelaere et al. 2003).

From a plant perspective, C flow into the rhizosphere can be considered as a cost for the plant, because a significant amount of C does not contribute to dry matter production. Thus, maintaining rhizodeposition during plant evolution should be balanced by expected benefits.

In natural terrestrial ecosystems (i.e. without major human impact, such as agroecosystems), mineral N can be a limiting factor for plant growth (Vitousek and Howarth 1991) and plants maintain interactions with soil microorganisms to enhance N nutrition. Non-specific interactions include the stimulation of microbial activities in the rhizosphere providing the essential energy to degrade soil organic matter and to remobilise some of the N immobilised in soil organic matter (Hodge et al. 2000). This stimulation of the mineralisation of soil organic matter following fresh organic matter inputs corresponds to the so-called 'priming effect' (Kuzyakov et al. 2000; Fontaine et al. 2003; Paterson 2003). The role of microorganisms in such priming effect is considered to be due to two separate mechanisms, depending on the species strategy (r or K) (Fontaine et al. 2003). (1) An increase in the release of extracellular enzymes by r-strategists; these enzymes are directed to fresh organic matter depolymerisation, but they can also degrade soil organic matter (mechanism 1). (2) The stimulation of K-strategists by metabolites released during the partial degradation of either fresh or soil organic matter by r-strategists, ultimately resulting in an enhanced mineralisation of the soil organic matter by enzymes produced by K-strategists (mechanism 2, implying co-metabolism between r-strategists and K-strategists). The priming effect in the rhizosphere is a direct consequence of rhizodeposition (Kuzyakov et al. 2000).

Exudates may enhance the activity of phosphate-solubilising bacteria, and hence increase the plant's P supply (Richardson 2001). Although the ability to solubilise phosphate is common in isolates from the rhizosphere, the application of these organisms as plant inoculants varies in its effectiveness (Kucey et al. 1989; Richardson et al. 2009). Inoculation of seeds of chickpea (Cicer arietinum) with phosphate-solubilising bacteria on agar plates, followed by growth in pots with sterilised vermiculite significantly

enhances plant growth and shoot P concentrations (Gull et al. 2004). Trials with wheat (Triticum aestivum) in pots with unsterilised soil showed that bacterial strains that are good at solubilising phosphate in laboratory tests result in increased grain yield and grain P content in the presence or absence of applied dicalcium phosphate (Harris et al. 2006). We are still a long way off application of phosphate-solubilising bacteria under real-world field conditions.

In addition to microorganisms that depend on the release of C in the soil surrounding the roots, a number of microorganisms occur in what is considered the inner rhizosphere, e.g., endophytes living in the root apoplast. These endophytes get first served upon the exudation of C from the surrounding root cells. Recent results by Deshmukh et al. (2006) show that some fungal endophytes, e.g., Piriformospora indica are beneficial to host crop plants (e.g., barley, Hordeum vulgare) via induced local and systemic resistance to fungal diseases and by increasing resistance to abiotic stress. These endophytes require host-cell death for proliferation in rhizodermal and cortical cells. Deshmukh et al. (2006) suggest that this endophyte interferes with the host cell-death program to form a mutualistic interaction with the plant host. The prevailing view of endophytic, symbiotic fungi is that selection pressures have imposed a directionality on the evolution of symbiotic lifestyles (Saikkonen et al. 1998). Accordingly, mutualistic endophytes would be expected to have evolved from parasitic or pathogenic fungi. However, some pathogenic Colletotrichum spp. have the ability to express different symbiotic lifestyles based on host genotypes in a single geographical location. A single fungal isolate may be pathogenic in some plant species, but provide mutualistic benefits such as disease resistance, drought tolerance, and growth enhancement to other plant species (Redman et al. 2001; Rodriguez and Redman 2008). According to these authors, either Colletotrichum spp. have evolved to possess maximum symbiotic flexibility or directional evolution has occurred in a host genotype-specific manner. Such observations warrant a re-evaluation of hypotheses describing the evolution, ecology, and dynamics of fungal and plant communities.

The best-documented case of endophytic fungi for which cost-benefit approaches have been developed is that of mycorrhizal fungi. The cost of such symbioses is especially well documented, the host plant deliver-

ing from 4 to 20% of the total C assimilated by photosynthesis. This means a significant cost in all cases (Peng et al. 1993; Rygiewicz and Andersen 1994; Tinker et al. 1994; Watkins et al. 1996). It is slightly more difficult to estimate the benefits for the plant which include increased access to poorly mobile soil resources such as P or micronutrients, if these nutrients are limiting growth. Resource limitation is indeed a key component of cost-benefit analyses of the mycorrhizal symbiosis (Johnson et al. 1997). When P is limiting, increasing the volume of soil from which P can be depleted (i.e. the volume of the rhizosphere) can be achieved at minimal extra C cost via root hairs. Conversely, mycorrhizal hyphae are likely more efficient, but also less cost-effective (Lynch and Ho 2005). Peng et al. (1993) showed that at high, non-limiting P supply, the growth of Citrus seedlings is significantly decreased as a result of mycorrhizal infection. Although many mycorrhiza researchers dislike describing some mycorrhizal interactions as parasitic, it is technically an accurate description of cases where the fungus is detrimental to the plant (Johnson et al. 1997).

From a microbial perspective, the rhizosphere is a niche of high microbial activity, due to the release of rhizodeposits, compared with the bulk soil, which is considered an oligotrophic environment limited by C. This leads to important modifications in the genetic structure and diversity of bacterial and fungal communities resulting from the competition between soil microorganisms for nutrients provided by plants (e.g., Mougel et al. 2006). Using different Arabidopsis thaliana accessions, Micallef et al. (2009) recently demonstrated that modifications of soil microbial communities are plant genotype-specific. This may offer the possibility to manage microbial communities in the rhizosphere.

As the flux of rhizodeposits corresponds to efflux and re-uptake of C, the plant plays an important role in the control of the soil food web, and also in the molecular control points for the co-evolution of plants and rhizosphere organisms. When considering the effect of C allocation to microbial populations, it is worth separating the effect on specific mutualistic and parasitic populations (endophytic life style) and on other components of microbial communities (rhizospheric life style). This separation is especially relevant when considering co-evolution (see section below), which correspond to evolutionary forces that

happen when different species have close ecological interactions. Additional research at the microbial community level is required to further our understanding of why high rates of rhizodeposition have been maintained during plant evolution.

Mutualistic and parasitic interactions

The term coevolution is used to describe cases where two (or more) species reciprocally affect each other's evolution. Coevolution is likely to happen when different species have close ecological interactions with one another. These ecological relationships include a number of interactions that occur in the rhizosphere, involving parasite/host, competitive species or mutualistic species. The most obvious and best-studied of these plant-microbe interactions are those with symbiotic mutualists and parasites. The ecological relationships, including mutualistic symbionts, can be classified into two broad types: protectors against pathogens and providers of nutrients, e.g., mycorrhizal fungi and N_2-fixing microorganisms (Reynolds et al. 2003). Spatial variation in the interactions between parasites (and symbiotic mutualists) and their hosts is thought to be a major force in coevolution and in generating biodiversity (Thompson 1999). Due to their faster generation time, microorganisms evolve faster than their hosts. A greater evolutionary potential of parasites and symbiotic mutualists leads to the general prediction that they should be locally adapted to their hosts, and that their fitness should decrease with distance of the host population (Ebert 1994, 1998).

Plants interact with two major types of mutualistic soil microorganisms: mycorrhizal fungi and N_2-fixing microorganisms. The AM association represents an ancient symbiosis (Table 1), with fossil evidence dating back 400 million years (Remy et al. 1994; Brundrett 2002) which has led to the idea that AM have contributed to the colonisation of terrestrial ecosystems by early land plants (Redecker et al. 2000) (Fig. 5). The coevolution of mycorrhizal fungi and roots is now well established in the light of evidence from palaeobotanical, morphological studies and DNA-based phylogenies (Brundrett 2002). Different types of mycorrhizas are recognised, the most common being arbuscular mycorrhizas, in which the fungi belong to the Glomeromycota (Schüßler et al.
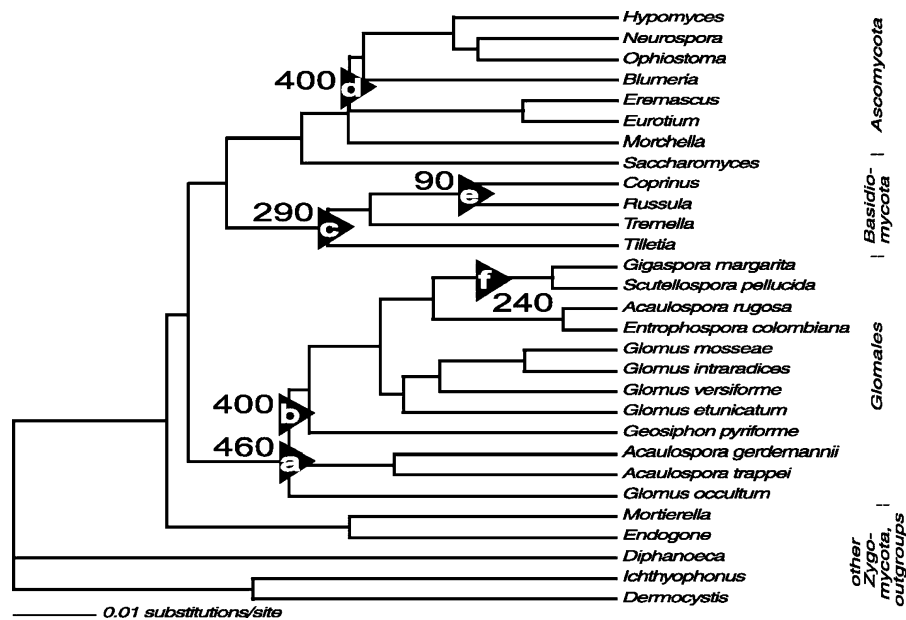
Fig. 5 Phylogenetic tree of fungi as constructed based on small subunit ribosomal sequences, with tree branching points referring to fungal fossils (letters *a* to *e*) and respective geological times indicated as numbers on the tree. From Redecker et al. (2000), Glomalean fungi from the Ordovician. Science 289:1920–1921. Reprinted with permission from AAAS. The *triangles* indicate that all fossils could also have been deposited later in the history of each clade, allowing the origins of the clades to be shifted back in time. Point *a* stands for the glomalean fossils reported in Redecker et al. (2000); point *c* stands for the fossil arbuscular mycorrhizas from the Rhynie Chert; point *c* indicates a fossil clamp connection (earliest evidence of Basidiomycota); point *d* indicates the Ascomycota from the Rhynie Chert; point *e* stands for the gilled mushroom in amber; point *f* indicates the arbuscular mycorrhizas of the Gigasporaceae type from the Triassic

2001), occurring in 92% of land plant families (Wang and Qiu 2006; Brundrett 2009), and the ectomycorrhizas, which occur in certain families of gymnosperms, dicotyledons and one monocotyledon genus (Brundrett 2002). There is a strong relationship between the age of plant-fungus associations and the degree of dependence of mycorrhizal fungi on their hosts, as all AM (about 400 million years old) and some ECM (about 100 million years old) are incapable of independent growth (Table 1).

Brundrett (2002) proposed the following order of evolution:

(1) Endophytic associations that could be considered as the source of new plant-fungus associations. The first stage of evolution from endophytic to mycorrhizal fungus would be specialisation of both partners; at this stage benefits to the plant would be limited.

(2) Mutualistic associations, where the exchange processes evolved to access limiting resources (mineral nutrients for the plant and C compounds for the mycorrhizal fungi). It is possible that the first mycorrhizas were formed by a Geosiphon-like fungus with an abundant supply of N obtained from associated cyanobacteria (Schüßler and Kluge 2000). In this context, both AM and ECM evolved as a complex interface with active exchange of limited duration. Increasing control of associations by the host along with increasing interface complexity are the strongest evolutionary trends.

(3) The third proposed stage of evolution consists of myco-heterotrophic plants where the fungi apparently do not benefit from the association with myco-heterotrophic plants, but where plants get C from their mycorrhizal associate, as occurs in orchids.

The Glomeromycota are a single unique ancient lineage, in contrast with other fungi that have multiple origins and coevolved with plants much more rapidly (Redecker et al. 2000; Schüßler et al. 2001). Some plants may continue to acquire new fungal lineages as for ECM where rapid diversification of these fungi continues to this day (Hibbert et al. 2000). Most

lineages of mycorrhizal fungi have descended from saprophytes with enzymes that can penetrate plant cell walls that presumably first became endophytes after attraction to roots by exudates (Kohzu et al. 1999). New types of mycorrhizas do not always result from the adoption of new lineages of fungi, as some myco-heterotrophs exploit ECM fungi or saprophytes. Orchid mycorrhizal fungi may not benefit from associations with orchids and thus would not co-evolve with plants, or form separate lineages from their saprophytic or parasitic relatives. This is in line with the prevailing view of a directionality of the evolution of symbiotic lifestyles, in which mutualistic endophytes are expected to have evolved from para-sitic or pathogenic fungi (Saikkonen et al. 1998). However, as discussed above, this view is currently challenged by the discovery of fungal endophytes that exhibit a whole array of lifestyles in a given environment, as a function of the host plant species that is colonised, the latter being responsible for the control of the fungal lifestyle (Redman et al. 2001).

N$_2$-fixing symbiotic associations include symbio-ses between Fabaceae and rhizobia, actinorhizal plants and *Frankia*, *Parasponia* sp. and rhizobia, and cycads and cyanobacteria. This cyanobacterial association is possibly the most ancient and could have evolved 250 million years ago (Raven 2002). Cycads represent an ancient life form and are the most primitive seed-plants, dating back to the mid-late Devonian, 380-360 million years ago (Brenner et al. 2003). They develop symbiotic associations with cyanobacteria, which evolved 3 billion years ago (Schopf et al. 2002), suggesting that competent cyanobacteria may have evolved well before the cycads did. However, compared with other symbio-ses, we know very little about this primitive form and how it has evolved. There is virtually no direct evidence for the origin and evolution of land plant/ cyanobacteria from fossil records. Krings et al. (2009) recently presented evidence for a filamentous cyano-bacterium associated with mycorrhizal axes of an Early Devonian land plant, *Aglaophyton major*. The cyanobacteria enter the plant through the stomata and colonise the substomatal cavity and intercellular spaces in the outer cortex. This is the earliest direct evidence for cyanobacterial associations with land plants.

In other symbiotic associations, the result of the plant-microbe interactions involves the formation of specific organs, called nodules (in legumes) or rhizothamnia (in actinorhizal species). Studies based on the chloroplast gene *rbcL* suggest that the flower-ing plant families involved in rhizobial or actinorhizal symbioses belong to the same large lineage, suggest-ing that a predisposition for forming nodules with rhizobia or rhizothamnia with actinorhizal bacteria has originated only once during the evolution flower-ing plant (Soltis et al. 1995). Nevertheless, phyloge-netic studies based on *rbcL* sequences indicate that the capacity to nodulate appeared at different times during plant evolution (Doyle et al. 1997). Genes involved in nodulation belong to multigene families with a complex evolutionary pattern as illustrated by leghaemoglobin genes (Clegg et al. 1997). I n *Vicia*, the most distantly related member of the globin gene is also induced in a mycorrhizal symbiosis, suggest-ing a connection between the two symbioses (Frühling et al. 1997). Origins of the legume, *Parasponia* and actinorhizal symbioses are considerably more recent than the cycad-cyanobacteria symbiosis, given that angiosperms did not evolve until 250 to 150 million years ago (Sprent and Raven 1992). Comparison of phylogenetic trees using representative *Frankia* (based on 16 S rDNA and *nifH* sequences) and actinorhizal plants (based on *rbcL* sequences) suggest some degree of coevolution (Jeong et al. 1997). Concerning the Fabaceae and rhizobia association, the coevolution process is less clear, as shown in the *Medicago-Sinorhizobium* association, despite the fact that cospeciation in *Sinorhizobium* and *Medicago* occurred (Béna et al. 2005). This result is not surprising, because coevolution is rare in associations in which the microsymbiont has a free-living stage (Ronquist 1998). Aguilar et al. (2004) suggested coevolution of *Phaseolus vulgaris* and *Rhizobium etli* in the centres of host plant genetic diversification, stressing the necessity to take into account the geographical pattern of local co-adaptation (Thompson 1997). More recently, in *Medicago truncatula* the ability to develop symbioses with both AM fungi and rhizobia involves some common genes (e.g., *DMI1*), pointing towards a common evolutionary pathway in the ability in *Medicago truncatula* to develop symbi-otic associations in the early stages of the interaction (Ané et al. 2004). Cospeciation of symbiotic partners involves stabilising mechanism (sanctions from plant partner) to maintain such association during evolution (Sachs et al. 2004). Theory predicts that mutualisms

may be evolutionary unstable because of higher fitness of 'cheater' genotypes (receiving greater fitness benefit than they confer) (Denison 2000). The presence of cheaters in rhizobium genotypes appears to be due to the symbiotic and saprophytic lifestyle of rhizobium genotype corresponding to horizontal transmission in which evolution of rhizobia could be influenced by plant functioning (in nodules) or the soil environment. Some evidence for adaptive partner choice, which might stabilise mutualims against the invasion of cheaters was reported in *Medicago truncatula*-rhizobium mutualism. These results stress the role of plants in the rhizobium genotype partner choice from soil diversity to reward more cooperative rhizobium strains (Heath and Tiffin 2007, 2009).

Parasitic associations between higher plants and microorganisms involve two independent sequences of infection processes corresponding to infectivity (infection success) and virulence (host damage). In plant pathology, virulence is synonymous with infectivity in accordance with classic gene-for-gene interactions where specific pathogen gene products trigger resistance reactions in the plant. Gene-for-gene is an important genetic system of interaction in coevolution between airborne parasites and plants (Thompson and Burdon 1992). In soil-borne parasites, mechanism of plant resistance or tolerance of parasites often involves complex genetic determinants, i.e. polygenic rather than monogenic resistance as for air-borne parasites.

Less is known about the role of plant genes involved in resistance or tolerance. In some cases resistance to soil-borne diseases is monogenic and dominant, as well as conferred through polygenic effects depending upon the physiological race of the microbial pathogen and the host plant genotype examined (Wissuwa et al. 2009). An interesting specificity in microbe-microbe, antagonistic interaction in the rhizosphere is the interactions of pathogens with beneficial microorganisms able to suppress disease with mechanisms like antibiosis, i.e. involving the production of antibiotics targeted against microbial pathogens, or competition for nutrients (Raaijmakers et al. 2009). Microbes that produce antibiotics are readily isolated from natural disease-suppressive soils, e.g., antibiotics against take-all of wheat (Weller 1988), black root rot (Keel et al. 1996), or *Fusarium* wilt (Tamietti et al. 1993). In addition, competition for C and Fe are also responsible for tolerance to *Fusarium*

wilt in disease-suppressive soils (Lemanceau and Alabouvette 1993). Microbial antagonism against parasites decreases the frequency of root infections and the severity of the disease in plants, whereas antagonism against deleterious microorganisms enhances plant growth (Schippers et al. 1987). Plant growth promotion can also be due to metabolites affecting the plant's physiology, e.g., growth substances (Glick 1995; Richardson et al. 2009). Specific bacterial metabolites may induce systemic resistance by eliciting defence reactions of the host plant (Van Loon et al. 1998). Much less is known about these beneficial plant-microbe interactions and in particular the plant genetic determinants to support or enhance them. Using a quantitative genetic analysis, some quantitative trait loci of tomato were identified in the interaction of a biocontrol strain (*Bacillus cereus*) and a parasite (*Pythium torulosum*). The corresponding traits identified were associated with the resistance to *Pythium torulosum*, growth parameters of the biocontrol strain, seedling emergence and microbial biocontrol (Smith et al. 1999). There is some evidence that modern breeding efforts in crop plants have inadvertently selected against hosting such beneficial microorganisms as documented for the AM symbiosis (Hetrick et al. 1995; Wissuwa et al. 2009). Further research is needed to explore possible coevolution between host plants and particular microbial populations or communities that are mutualistic but not symbiotic.

Soil formation, biogeochemical cycling and Earth history

Given the many ways roots and rhizosphere microorganisms interact with soil properties, one may ask: what would a soil be like in the absence of plants? More to the point: would there be any soil in the absence of plants? Studying the first steps of colonisation by plants of bare rocks (such as glacial moraines or basalt flows) provides some answers to these questions (Cochran and Berner 1996). While rock-lichen interactions have received more interest as a model of biological weathering (Drever 1994; Banfield et al. 1999), Cochran and Berner (1996) and Moulton et al. (2000) stress that much higher weathering rates are achieved once the basalt rock had been colonised by higher plants, compared with that of bare rock or rock covered with lichens. There have

also been experimental approaches to show that roots and their associated microorganisms can considerably increase the rate of weathering of rocks (Bormann et al. 1998; Hinsinger et al. 2001) or minerals (Hinsinger et al. 1993; Bakker et al. 2004; Calvaruso et al. 2006). Based on such observations and measurements, it is concluded that higher plants play a pivotal role in soil formation in the root/rock interface, i.e. the very first stage of a rhizosphere can be considered as the site where soil formation actually starts.

From an evolutionary perspective, the emergence of vascular plants, and, amongst these, of higher plants with deep and mycorrhizal root systems, is considered a major process in the Earth history and the biogeochemical cycles of CO_2 (and O_2) via their impact on rock weathering and soil formation in terrestrial ecosystems (Berner 1992, 1997; Kenrick and Crane 1997; Retallack 1997; Beerling et al. 2001; Beerling and Berner 2005; Taylor et al. 2009). Whilst the considerable decrease in atmospheric CO_2 concentration during the Devonian period (410 to 360 million years ago) was due to higher plants locking C up in their large trunks and leaves, even more significant was the role of roots (Kenrick 2001).

The removal of enormous quantities of CO_2 from the Devonian atmosphere is now thought to be the consequence of the development of deep-rooted plants that have contributed to achieving: (1) the formation of cracks and mechanical breakdown of rock particles as a consequence of root growth, with potential consequences for the circulation of water throughout the profile, its residence time and the overall water cycle; (2) an input of C deep in the regolith, thereafter creating the soil and subsoil profile, allowing microorganisms to grow at greater depth, along with root growth; and (3) the chemical changes of their rhizosphere, as a consequence of water and nutrient uptake, respiration, exudation of acidic and chelating compounds (Hinsinger et al. 2006, 2009). These various processes are not all equally well documented, especially on long (evolutionary) time scales.

Root-induced physical breakdown of rocks and consequences for deep soil formation and the water cycle

The colonisation of the terrestrial environment by plants profoundly modified the landscape, the soils and terrestrial ecosystems, and at an even broader scale the composition of the atmosphere. Phylogenetic studies favour a single origin of land plants from Charophyceae, which are predominantly freshwater green algae from the mid-Paleozoic era (Kenrick and Crane 1997). During the early Devonian period, the terrestrial vegetation would have looked like a more or less continuous short chlorophyllous carpet, largely composed of bryophytes, and other plants that did not have roots, but rhizomes instead. Plant cover consisted of rather short shoots erected along those running stems.

Plants with roots appeared in the late Devonian and more so during the Carboniferous period (starting 360 million years ago), with the most primitive being pteridophytes (ferns), horsetails and cycads (Kenrick and Crane 1997; Brundrett 2002). The rooting depth and root diameters significantly increased over the late-Devonian to early-Carboniferous transition period (Retallack 1997) (Fig. 6). The differentiation of roots presumably resulted from an adaptation to the new organo-mineral medium, porous, wet and relatively nutrient-rich. Major functions of roots are to acquire water and mineral nutrients for the plant, and to exude organic compounds, allowing the growth of significant microbial communities in the rhizosphere. Even the oldest fossils of roots show traces of close associations with fungi resembling AM (Brundrett 2002).

Evidence for endophytic associations is available for the first bryophyte-like land plants, which may have been the precursors of the first mycorrhizas (hyphae, vesicles and arbuscules) reported to occur in fossil rhizomes (Brundrett 2002) in the early Devonian, i.e. in land plants that had no roots, and thus no rhizosphere. From this time onwards, the interactions between plants, soil and microorganisms had the same significance ascribed to them today. Each component interacted with the others, plant-soil and microorganism-soil, while plants and microorganisms coevolved; these types of interactions have persisted ever since. The evolution of strong, deep, mycorrhizal root systems of vascular plants started at this period and occurred to a large extent over the late Devonian-early Carboniferous transition period (Kenrick and Crane 1997; Retallack 1997; Brundrett 2002; Taylor et al. 2009) (Fig. 6); their adaptation to most climatic and pedological conditions found on Earth contributed to the colonisation of continental surfaces (Kenrick and Crane 1997).
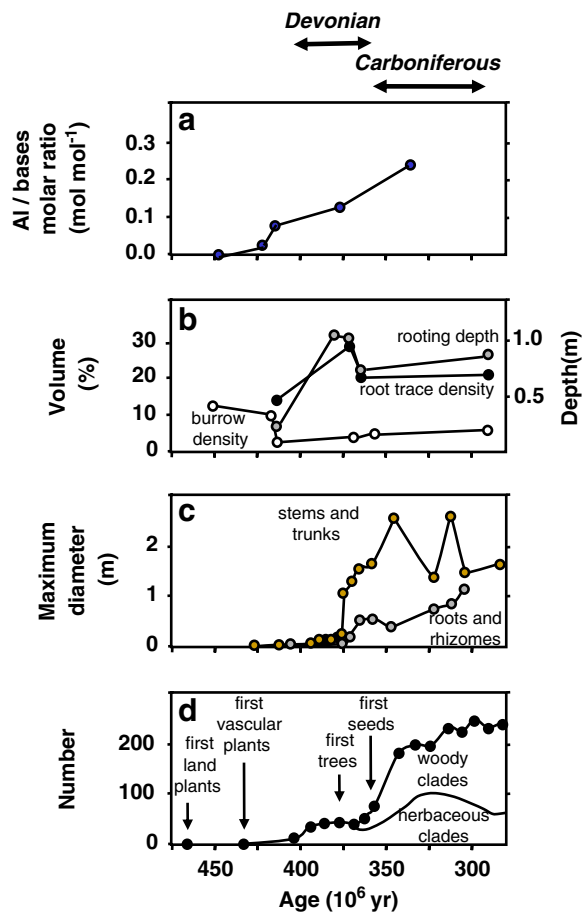
Fig. 6 Evolution of paleosol features in the mid-Paleozoic period (modified after Retallack (1997) Early forest soils and their role in Devonian global change. Science 276:583–585. Reprinted with permission from AAAS). Index of subsurface silicate weathering as assessed by the molar ratios of aluminium/bases in subsurface minus surface horizons (a), indices of bioturbation, as assessed along a line transect of hand specimens occupied either by burrows or by roots (expressed as volume percent), and corresponding root depth (b), as related to the maximum diameter of fossil stems and trunks, or of roots and rhizomes (c) and diversity of fossil plant species records, as expressed as numbers of species (d)

Plant cover plays several major roles on the surface of the continents (Berner 1997). Most significant is to limit erosion via retaining and fixing the fine, organic and mineral particles. These fine particles, clay- and silt-sized minerals and organic matter, have a high specific surface area and exchange capacity. They are organised in aggregates, which are physically stabilised, contributing to soil structure. A well structured soil supports deep rooting of plants which itself contributes to stabilise and structure the soil. The

retention of fine particles by plant cover thus results in a perpetuating cycle, which finally benefits both plant cover and soil formation (Van Breemen 1993). The soil structure is important for biological activity by providing a stable habitat to all soil-borne organisms, and by allowing the transfer of water and exchange of gases involved in respiratory processes. It also allows infiltration of water. This soil water-retention capacity contributes locally to the maintenance of conditions favourable for the development of roots and other biological activities. At a larger, regional scale, the development of higher plants has played a key role in regulating water flows and limiting erosion processes (Berner 1997).

The property of plants to improve soil structure, or to increase the porosity of degraded horizons, is widely used in agronomy and ecological engineering. Blanchart et al. (2004) studied the effect of various cultural practices on the change of the physical properties of vertisols degraded by intensive gardening. They showed that a culture of the grass *Digitaria decubens* during 4 years made it possible to double the porosity of the top 40 cm of the soil. At the same time, the proportion of stable aggregates increased from less than 30 to nearly 70% which resulted in a 50% reduction of surface erosion. Consequently, the content of soil organic C increased from 15 to 25 g kg^{-1} soil. Akhter et al. (2003, 2004) used different methods to improve the physical properties of degraded sodic soils. They showed that a culture of kallar grass (*Leptochloa fusca*) significantly increased porosity, water retention, permeability and structural stability of soils. The effects were significant as of the third year of culture, and increased the following years. In this case, again, the improvements coincided with a significant increase in the soil organic matter content. In such soils, which often exhibit physical constraints at depth which limit the infiltration of water and root growth, young roots tend to re-use former root chanels (Creswell and Kirkegaard 1995), resulting in cumulative rhizosphere effects (Pankhurst et al. 2002; Hinsinger et al. 2005). Jassogne (2008) has recently shown that in such environments some plant species play a key, pioneer role in creating new biopores in the heavily textured soil horizons that limit the growth of other plant species; these biopores can subsequently be re-used by roots of primer plant as well as other plant species. The concept of primer plants, as defined by Yunusa and Newton (2003) for

such environments, would be worth being extrapolated to other physically contrained environments, in line with the concept of ecosystem engineers, *sensu* Jones et al. (1994).

The effect of plant growth on soil structure occurs at the same time at different scales. At the scale of a single root, the growing root leads to aggregation of the surrounding soil particles (Hinsinger et al. 2009). In 1862, Sachs (quoted by Dehérain 1873) showed that soil binds to the youngest parts of the root system of wheat (*Triticum aestivum*), forming a rhizosheath. This rhizosheath results initially from physical interactions between the root and the soil, via root hairs or mycorrhizal hyphae, which emerge from roots (Dorioz et al. 1993; Czarnes et al. 1999; McCully 1999). It also results from the exudation of polysaccharides by roots or associated microorganisms. Exudation, root-hair growth and mycorrhizal infection occur especially in the youngest region of the roots which explains Sachs's observation and those of many authors since. Note that this first effect of binding of rhizosphere particles may be followed by a secondary effect; namely, that organic matter may decrease the wettability of aggregates which slows their rate of wetting and thus decreases the intensity of constraints that act inside the aggregates and tend to disrupt them (Chenu et al. 2000).

Root-induced and microbially mediated sequestration of C as organic matter and carbonates and consequences for the global C cycle

The input of C into the soil at greater depths than achieved by the pre-Devonian vegetation comprising non-rooted plants is a major root-induced process, which dramatically influenced the Earth history via its impact on global pedogenesis. The consequence of the advent of higher plants in the Paleozoic (542–251 million years ago) on the biogeochemistry of C has become a hot topic, given its relevance for better understanding the biogeochemical cycle of C and its link with elevated CO_2 concentrations in the atmosphere (Berner 1992, 1997; Mora et al. 1996; Beerling et al. 2001; Beerling and Berner 2005). Indeed, the atmospheric CO_2 concentration dropped from 3000–4500 µmol mol^{-1} in the early-mid Devonian (410–380 million years ago) to about 1000 µmol mol^{-1} towards the end of the Devonian (360 million years ago) (Fig. 7a). That coincided with the advent of

deep-rooted vascular plants, which were mainly responsible for this dramatic global change (Berner 1992, 1997; Retallack 1997; Beerling and Berner 2005) (Figs. 6b and 7b).

Beerling and Berner (2005) concluded that the decrease in atmospheric CO_2 concentration was due to enhanced rates of photosynthesis, and subsequent sequestration of C into the soil (Fig. 6c), burial of C into sediments, and enhanced weathering of Ca- and
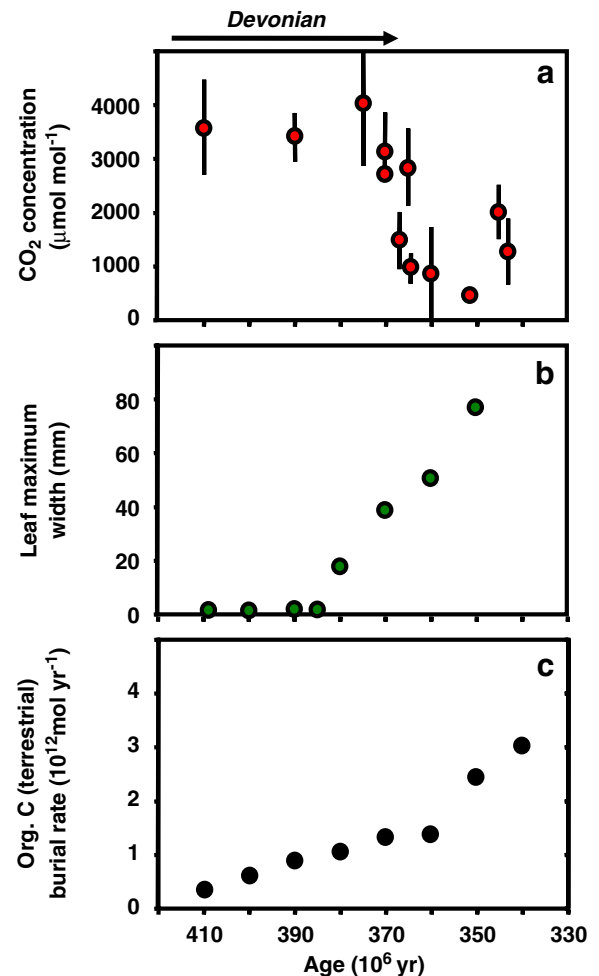
Fig. 7 Changes in the atmospheric CO_2 concentration during the Late Palaeozoic (**a**), concurrent increase in maximum width of megaphyll leaves calculated from fossils for 10 million year intervals (**b**), and changes in terrestrial carbon burial, calculated as the difference between global and marine burial (**c**), the latter being estimated from pyrite burial rates and a Cambrian–Silurian mean molar organic carbon/pyrite sulfur burial ratio of 1.5 (adapted from Beerling and Berner 2005, with kind permission from the The National Academy of Science of the USA)

Mg-bearing silicates, leading ultimately to the formation of Ca- and Mg-carbonates in the oceans. This input of C is linked with the decay of deep roots, as accounted for by models such as those developed by Berner and Kothavala (2001) and Beerling and Berner (2005). The role of root and microbial respiration in the rhizosphere should also be acknowledged, given its expected impact on the rates of dissolution (weathering) of minerals such as silicates and carbonates (Retallack 1997; Kuzyakov et al. 2006; Taylor et al. 2009). The additional input of C linked with rhizodeposition and the subsequent microbial loop needs to be accounted for in biogeochemical models used for reconstructing the C history of the Earth, as current knowledge of rhizodeposition shows it is of similar magnitude as C investment in root architecture (Nguyen 2003; Jones et al. 2004, 2009).

Via their direct role in the formation of biogenic carbonates, i.e. the precipitation of $CaCO_3$, predominantly calcite, which ultimately forms calcretes (Freytet et al. 1997; Verboom and Pate 2006a, b), roots of higher plants can leave long-lasting morphological features in soil profiles and be a major contributor to pedogenesis. Calcareous rhizoconcretions have been observed in some of the oldest paleosoils as described by Retallack (1997), who stressed "the early Paleozoic greenhouse may have been curbed by the evolution of rhizospheres with an increased ratio of primary to secondary production and by more effective silicate weathering". A first type of biogenic precipitation of calcite in the rhizosphere is related to the build-up of Ca which results from the large amount of Ca transferred towards the root surface as a consequence of mass flow (Jaillard 1982; Callot et al. 1983; Hinsinger 1998). In calcareous soils, this process can lead to the precipitation of calcite crystals around the roots which remains clearly visible around root pores once the root has died (Fig. 8a). Ultimately, the coalescence of the calcite precipitates around neighbouring roots can result in continuous calcrete formation when root density is large and ambient conditions are prone to biogenic precipitation of Ca carbonate in the rhizosphere (Jaillard 1982; Callot et al. 1983). This process is very clearly illustrated in 'The Pinnacles', 200 km north of Perth in Western Australia, where the soil was blown away following a bushfire, exposing the calcrete formations formed around roots over many years before (Fig. 8b).
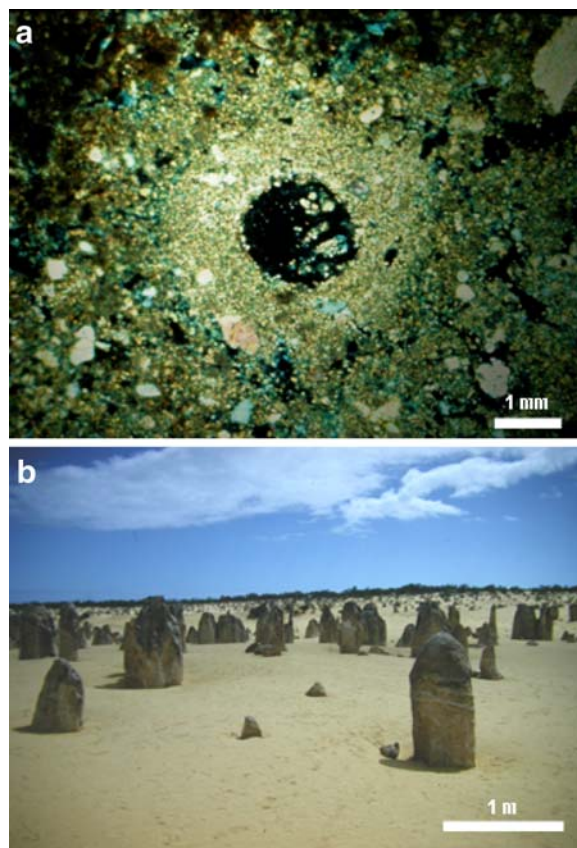
Fig. 8 Root-induced calcrete formation as a result of calcium carbonate (calcite) precipitation around a peach (*Prunus persica*) root biopore (reproduced from Callot et al. 1983, with kind permission of INRA Publishers) as a consequence of mass-flow and increased concentration of Ca ions in the rhizosphere (**a**) and remnant calcrete formations presumably formed around tree roots after the soil was blown away following a bushfire, exposing the so-called 'Pinnacles' in Nambung National Park (**b**), 200 km north of Perth in Western Australia (photo by Philippe Hinsinger)

Although it is not as strictly related to rhizosphere processes as the example illustrated by 'The Pinnacles', Jaillard (1982, 1983, 1984, 1985) and Jaillard et al. (1991) have described another fascinating case of biogenic precipitation of calcite induced by root activity, leading to the formation of calcified roots in calcareous soils. These calcified roots, when fully preserved in the soil, occur and appear as calcite crystals shaping the root cortex cells, while the stele remains free of precipitates (Fig. 9). This process occurs in living plants, and is therefore not a fossilisation process (Jaillard 1987a, b). It is actually promoted by root activity, which can dissolve

Fig. 9 Root-induced calcrete appearing as calcified roots forming as a result of calcium carbonate (calcite) precipitation in the cortical cells of perennial grasses growing in the 'garrigues' Mediterranean bush North of Montpellier in calcareous soils developed on a calcareous marl parent material (photo by Philippe Hinsinger) (**a**), closer view under light microscope showing distinctly that the stele is not calcified (**b**), and scanning electron micrograph of two rows of calcified cortical cells (**c**) (taken from Jaillard et al. 1991, with kind permission of Elsevier Ltd.)

abundant amounts of Ca carbonates in the outer rhizosphere as a consequence of respiration and proton release, and alleviate Ca toxicity by precipitating it as calcite in the vacuoles of root cortical cells (Jaillard 1987a, b). Although root-induced, this biogenic process is not just a rhizosphere process as it occurs inside root cells, similarly as the well documented precipitation of Ca oxalate (Horner and Wagner 1995). However, Ca oxalate formation seldom occurs to the same extent as found for calcite, which ultimately can completely fill the vacuole and the cell, so that the whole cortex tissue is full of large crystals shaping each individual cell. Remarkably, Jaillard (1984) showed that this biogenic process is responsible for a considerable shift of the particle size

of calcareous soils, because of the rather isometric size of the calcified cells (around 80 µm diameter). Jaillard (1984) calculated that within about 1000 years, a third of all the Ca carbonate contained in calcareous soils can be dissolved and re-precipitate due to root activity. This process is thus one of the most dramatic cases of biogenic mineral formation in terrestrial ecosystems.

It should be stressed that the process of re-precipitation of Ca carbonate is a redistribution of previously existing Ca carbonate, and thus it does not involve any net C sequestration in the soil. That is, the dissolution of Ca carbonate in the rhizosphere is compensated for by re-precipitation inside the root cells. Based on the measurement of ^{14}C incorporation

in Ca carbonate derived from ^{14}C-labelled root exudates, Kuzyakov et al. (2006) calculated that full re-crystallisation of loess carbonate would take 400 to 2000 years, which is fairly close to the estimated 1000 years provided by Jaillard (1984). This root-borne phenomenon may also account for the formation of widespread fossils that are especially abundant at the Cretaceous-Tertiary junction, the so-called microcodium, as suggested by Jaillard et al. (1991) and subsequently substantiated by Kosir (2004). Using morphological and isotopic geochemical approaches, these authors demonstrated that microcodium has many similarities with present-day rhizomorphic calcretes (Jaillard 1987a, Jaillard et al. 1991; Morin 1993), confirming early views of Klappa (1980). Such features, called rhizoliths, can be well preserved in paleosols and ancient calcretes (e.g., Retallack 1997). They have recently been used by Wang and Greenberg (2007), because they provide a high-resolution and continuous record of paleoclimates and past environments, based on isotopic geochemistry.

The formation of Ca oxalate crystals is well documented for ectomycorrhizal and saprophytic or pathogenic fungi, amongst which some species produce massive amounts of oxalic acid (Cromack et al. 1979; Dutton and Evans 1996; Connolly et al. 1999; Wallander 2000; Casarin et al. 2004), with a potential impact on the weathering of silicate minerals (Paris et al. 1996; Wallander 2000). This occurs in the rhizosphere as related to the activity of ectomycorrhizal fungi (Lapeyrie 1988; Wallander 2000; Casarin et al. 2003, 2004), especially in calcareous soils (Casarin et al. 2003), where the crystals of Ca oxalate may ultimately develop into needle-shaped crystals of Ca carbonate (Callot et al. 1985a, b; Verrecchia 1990; Verrecchia and Dumont 1996). The latter process would hardly change soil mineralogical composition or contribute any net sequestration of atmospheric C when the predominant source of Ca is the dissolution of soil Ca carbonate as would be the case for calcretes formed in calcareous soils. However, it may well be the case when the source of Ca is the weathering of other Ca-bearing minerals, e.g., plagioclase feldspars (Cromack et al. 1979; Landeweert et al. 2001). If so, the role of Ca oxalate in biogeochemical cycles as described by Graustein et al. (1977) should be reconsidered, as pointed out by Cailleau et al. (2004).

Root-induced and microbially mediated weathering of rocks and minerals and consequences for the cycle of nutrients and soil formation

The contributions of higher plants and soil microorganisms to the weathering of primary silicate minerals and rocks are manifold, and largely based on rhizosphere processes. Weathering models now account for the additional effect of plants due to the uptake of nutrients forming silicate minerals and rocks (e.g., Taylor and Velbel 1991; Bormann et al. 1998; Moulton et al. 2000; Velbel and Price 2007). However, they do not fully account for all other rhizosphere processes likely to dramatically influence the weathering rates. While the role of roots and rhizosphere microorganisms on elevated soil CO_2 concentrations via respiration and exudation of organic acids is well acknowledged, the potential impact of protons and siderophores released by roots and rhizosphere microorganisms on the weathering of silicate rocks is poorly accounted for.

Hinsinger and Jaillard (1993) showed that the uptake of K by roots of ryegrass (*Lolium multiflorum*) and the subsequent depletion of K in the rhizosphere (decrease in solution K concentration) is the driving force for the weathering of a Mg-bearing silicate such as phlogopite mica and concurrent formation of a clay mineral (vermiculite) in the absence of any pH decrease. Hinsinger et al. (2006) showed that the sink effect of plant roots for K leads to an approximately 5- and 6-fold increase of the rate of release of interlayer K, and of the concurrent weathering of micas such as phlogopite and biotite, respectively, compared with unplanted systems where only leaching is responsible for the observed weathering. This agrees with weathering rates of biotite computed by Taylor and Velbel (1991) and Velbel and Price (2007), who showed that taking account of the uptake of K by the vegetation of forested watersheds leads to rates that are up to 3.5 times greater than when ignoring this term in the K budget. This rhizosphere process, which is simply the consequence of the uptake activity of plant roots is also the only one reconciling K budgets of long-term field trials conducted by agronomists, and current knowledge of soil mineralogy and chemistry. Indeed, fertiliser trials conducted in Europe have often shown that, in the absence of fertiliser K application, the cumulated removal of K by successive crops usually does not match with an

equivalent decrease in exchangeable K, even when this pool is considered as the bioavailable K for crops. Such field trials suggest that the release of non-exchangeable K amounts to 10 up to 100 kg K ha^{-1} yr^{-1}, as an average value computed over the whole duration of these long-term (several decades) fertiliser trials (Hinsinger 2002). Holmqvist et al. (2003) and Simonsson et al. (2007) found similar rates of weathering in long-term K-fertiliser trials of Northern Europe, pointing to an important contribution of the concurrent release of non-exchangeable K to the overall soil K budget. This contradicts current opinions of soil scientists that in such arable soils, the release of non-exchangeable K is negligible, because of the bulk soil solution K concentration typically ranging from 100 to 1000 µM.

The release of non-exchangeable K, which is actually largely based on the release of interlayer K and concomitant weathering of micas and micaceous clay (illite-like) minerals is governed by soil solution K concentration. Springob and Richter (1998) have clearly shown that the rate of this process is dramatically enhanced at soil solution K concentrations below 3 µM, and almost nil at those concentrations common in bulk soils of arable land in Europe. Based on such findings, virtually no release of non-exchangeable K is expected, although short-term pot experiments (Kuchenbuch and Jungk 1982; Niebes et al. 1993; Coroneos et al. 1996) as well as long-term fertiliser trials (Hinsinger 2002) have shown that this process may contribute a major proportion of K uptake by crops. The explanation lies in the specific chemical conditions of the rhizosphere. Claassen and Jungk (1982) showed, indeed, that while bulk soil solution K concentrations are in the order of several hundreds of µM, in the immediate vicinity (about 1 mm) of maize (Zea mays) roots, such concentrations could be as low as 2–3 µM. The latter are compatible with large rates of release of non-exchangeable K, as shown by Springob and Richter (1998). Therefore, as shown for single minerals (Hinsinger and Jaillard 1993), the sink effect of plant roots and subsequent depletion of soil solution K in the rhizosphere is the driving process that leads to the release of interlayer K and concomitant weathering of micaceous minerals in soils (Hinsinger 2002).

A recent study by Barré et al. (2007a) has further shown the causal link between these two processes,

with a quantitative assessment of X-ray diffraction data. These authors showed that the uptake of K by ryegrass (Lolium multiflorum) in a rhizobox experiment quantitatively matches the increased amount of interstratified illite-smectite minerals in the rhizosphere which formed at the expense of the illite-like clay minerals. These findings confirmed previous findings of Hinsinger and Jaillard (1993), with a similar approach applied to a single micaceous mineral instead of a whole soil clay fraction, as well as the earlier report of an increased amount of interstratified illite-vermiculite minerals in the rhizosphere of field-grown maize plants (Kodama et al. 1994). Applying the same method to soil clay fractions collected in a long-term fertiliser trial, Barré et al. (2008) confirmed on a longer time scale that plant uptake of K matches the formation of interstratified illite-smectite minerals at the expense of the illite-like clay minerals, as a consequence of the release of interlayer, non-exchangeable K from the latter. According to these authors, plants thus play a major role in the biogeochemical cycle of K and in the formation and dynamics of expandable clay minerals (vermiculites or smectites) in top soils, with illite-like clay minerals playing the role of a huge K reservoir (Barré et al. 2007b, 2008). Indeed, no release of interlayer K contained in micaceous minerals would be expected to occur in the absence of plants and the efficient sink effect of their roots depleting soil solution K in the rhizosphere. This shows that through rhizosphere processes, higher plants are major drivers of weathering of rocks and formation of soils.

As pointed out by Taylor et al. (2009) and Hinsinger et al. (2006), rhizosphere acidification should be taken into account when considering the relevance of rhizosphere processes in bulk soil formation (pedogenesis), as expected given that pH has a dramatic impact on the rate of weathering of most minerals, especially in the acidic range (Banfield et al. 1999). The role of pH in the biologically mediated dissolution of minerals as related to the production of organic acids by roots and rhizosphere microorganisms has been studied in detail for forest tree seedlings for various silicate minerals (Wallander and Wickman 1999; Bakker et al. 2004). Wallander and Wickman (1999) showed that ectomycorrhizal fungi are largely responsible for the observed elevated concentrations of citric and oxalic acids, which account for the release of K and Mg from biotite.

These studies did not distinguish the direct pH effect from that of the chelating carboxylates, which also directly impact dissolution/weathering reactions (Huang and Keller 1970; Jones et al. 1996; Jones 1998). Several studies show rhizosphere acidification in forest stands measured in situ, with potential consequences for accelerated weathering rates (Courchesne and Gobran 1997; Turpault et al. 2005), although such studies do not demonstrate the causal relationship between these two processes. The impact of pH changes on the weathering of micas and feldspars in the soil around ectomycorrhizal fungi was, however, clearly shown by Arocena et al. (1999) and Arocena and Glowa (2000). Some ectomycorrhizal fungi supposedly play a major role in these processes, rather than the host plant itself (Landeweert et al. 2001; Hoffland et al. 2004). Fungal hyphae are able to dissolve silicate minerals, thereby forming tunnel-like pores inside mineral grains (Jongmans et al. 1997).

When considering the potential involvement of ectomycorrhizal fungi in soil formation over longer time scales, we have to be aware that ECM occur only in a small proportion of all species among angiosperms and gymnosperms. They have evolved rather recently, compared with AM (Table 1); they first appeared around 100 million years ago (Brundrett 2002), and thus are not old enough to have contributed to a major extent to the enhanced weathering that occurred in the late Devonian with the advent of rooted vascular plants (Landeweert et al. 2001). On the other hand, AM fungi (Glomeromycota), which belong to a less diverse group than ectomycorrhizal fungi, evolved prior to the advent of deep-rooted vascular plants, 380 to 360 million years ago (Brundrett 2002; Beerling and Berner 2005; Taylor et al. 2009). However, their direct involvement in the weathering of rocks and minerals is questionable. This means that the enhanced weathering that occurred prior to the evolution of ectomycorrhizal fungi resulted likely from root-borne processes or non-symbiotic rhizosphere microorganisms, rather than mycorrhizas. Thus, the involvement of mycorrhizal fungi in the weathering of rocks and pedogenesis, and especially that of ectomycorrhizal species associated mostly with temperate, forest tree species, is of major importance in forest ecosystems, but restricted to the last 50–100 million years (Landeweert et al. 2001).

Another point when considering the implication of mycorrhizas in biological weathering is the potential role of bacteria associated with ectomycorrhizal roots and hyphae (Calvaruso et al. 2007; Uroz et al. 2007). Frey-Klett et al. (2005) reported selection of so-called mycorrhiza-helper bacteria belonging to fluorescent pseudomonads in ECM. Calvaruso et al. (2007) have shown that several ectomycorrhizal symbioses select for different bacterial communities that are potentially involved in the production of acidic or chelating metabolites, ultimately affecting the weathering of minerals. They also found that more bacteria exhibiting a large weathering potential were found in the ectomycorrhizosphere than in the bulk soil. This was confirmed by Uroz et al. (2007), who assessed the weathering capacity as the ability to acidify the growing medium and to release Fe from biotite particles in the growing medium. Among 61 isolates collected from Scleroderma citrinum mycorrhizas, mycorrhizosphere and adjacent bulk soil in an oak (Quercus petraea) forest stand, they identified bacteria of the Burkholderia, Collimonas, Pseudomonas and Sphingomonas genera, with the largest weathering capacity shown by the Burkholderia and Collimonas genera. Calvaruso et al. (2006) inoculated pine (Pinus sylvestris) seedlings with three strains of Burkholderia glathei amongst the most efficient isolates identified by Uroz et al. (2007) and measured the weathering of biotite in microcosms, based on Mg and K release rates. The weathering rate was increased 1.4-fold for Mg and 1.5-fold for K, when compared with that of pine alone, indicating a congruent dissolution, likely mediated by a proton- or organic acid-promoted dissolution of the mineral.

As in the recent study of Uroz et al. (2007), Leyval and Berthelin (1989, 1991) had shown earlier with axenic pine seedlings inoculated with an ectomycorrhizal fungus and rhizobacteria that the weathering of biotite is largely due to the effect of the host plant itself, with a substantial additional effect of rhizosphere microorganisms. This was even more so for a similar microcosm study conducted with maize and an AM fungus with or without additional effect of inoculated bacteria (Berthelin and Leyval 1982; Leyval et al. 1990); the host plant is responsible for the largest portion of the biologically mediated weathering of biotite, as shown by the release of K and Fe.

Although previous studies assessing the effect of plants and rhizosphere microorganisms on the bio-

logically mediated weathering of minerals have often stressed the microbial contribution, many have actually shown that the higher plants *per se* induces a major shift in the rates of weathering, relative to abiotic weathering. This might explain why the advent of vascular plants had such a dramatic effect on the weathering of silicates (Fig. 6a) as indicated by the decrease in atmospheric CO_2 concentration in the late Devonian (Fig. 7a) (Berner 1997; Retallack 1997; Beerling and Berner 2005). Biogeochemical models, however, attribute the effect of those plants to: (1) acidification of the rhizosphere as a consequence of respiration and the production of organic acids (assuming that these are largely due to rhizosphere microbial activities); and (2) the higher rate of uptake of nutrients from nutrient-bearing minerals (Beerling and Berner 2005), but the latter effect is seldom stressed.

In addition to its potential direct effect on shifting the dissolution equilibrium as clearly shown for K in micas (Hinsinger and Jaillard 1993), the uptake of nutrients by higher plants has a major effect on rhizosphere pH, excess cation over anion uptake resulting in proton efflux from roots and thus in rhizosphere acidification (Hinsinger et al. 2003). When one considers proton sinks and sources in terrestrial ecosystems, the balance of cations over anions taken up by the vegetation is, indeed, a major contributor (cation uptake being a source, while anion uptake is a sink for protons), sometimes greater than respiration and the resulting build-up of soil CO_2 concentrations (Van Breemen et al. 1984; Bourrié and Lelong 1994; Frey et al. 2004). This is especially so in acidic environments where respiration has little impact on pH, as opposed to the situation in neutral or alkaline environments. It should also be borne in mind that the proton-promoted dissolution of minerals is a major proton sink in terrestrial ecosystems (Van Breemen et al. 1984) which means that the weathering of rocks may mask the actual pH changes occurring in the rhizosphere, thereby hiding the actual importance of such a phenomenon (Hinsinger et al. 2003). This was also stressed by Hinsinger et al. (2001), who studied the weathering of a basalt rock in a microcosm study. They showed that, while a planted system leads to 2- to 10-fold increased dissolution rates for most elements (Ca, Mg, Si), compared with unplanted systems, where only leaching is responsible for the observed weathering, the impact of the plants on Fe-dissolution rates is much greater, up to 500-

fold. A significant root-induced acidification was observed which possibly explains the kinetics of release of Ca and Mg from the basalt, but obviously not that of Fe. Although Hinsinger et al. (2001) did not demonstrate the underlying processes, it is likely that the much greater effect for Fe than for other elements is due to more specific rhizosphere processes, rather than shifting the dissolution equilibrium via plant uptake and root-mediated acidification, e.g., redox changes or Fe chelation by root or microbial siderophores. This is also suggested by results obtained for the rhizosphere of various crop species supplied with goethite (a poorly soluble Fe oxyhydroxide) as sole source of Fe (Bertrand et al. 1999; Bertrand and Hinsinger 2000). Recently, Reichard et al. (2005) provided direct evidence for the involvement of phytosiderophores secreted by wheat (*Triticum aestivum*) in the ligand-promoted dissolution of goethite. A similar mechanism operates for microbial siderophores (Reichard et al. 2007).

Pate et al. (2001) noted a close association of species belonging to the Proteaceae and lateritic soils. As discussed above, almost without exception, species of the Proteaceae produce proteoid root clusters, which release vast amounts of carboxylates (Shane and Lambers 2005b). These carboxylates chelate Fe and other micronutrients which explains why Mn concentrations in cluster-bearing species tend to be high (Gardner and Boundy 1983; Bolland et al. 2000) and correlated with the fraction of the total root mass invested in cluster roots (Shane and Lambers 2005a). Pate and coworkers proposed that Fe is solubilised during the wet season, and then moves down the profile, where it is precipitated following microbial breakdown of the chelating carboxylates, giving rise to a lateritic or podzolic subsoil. This clearly shows that plants, through their exudation of specific compounds, can give rise to a subsoil that is very hard to penetrate, except through cracks and biopores, this hardpan being composed in this case of a ferricrete (Verboom and Pate 2003).

In later work, Verboom and Pate (2006a, b) propose that precipitates of silcrete, calcrete and ferricrete are formed in analogous manners, but further work is required to find out which exudation or other root-induced processes, if any, are involved in these pedogenic processes. This has been discussed above for the case of calcretes. Verboom and Pate (2006b) recently showed that in a similar environment

and with similar parent material, the occurrence of calcretes spatially coincide with myrtaceous woodland, while ferricretes are predominantly found under proteaceous shrub-heathland. This led Verboom and Pate (2006a) to further develop their 'phytotarium' concept, to emphasise the major role of the vegetation cover on soil profile development. Particularly remarkable evidence of bioengineered ferricretes are Fe-coated root channels that are recorded in lateritic or deep podzolic soil profiles (Verboom and Pate 2006a), as evidenced by the pale brown to red colour around root channels or around roots growing both vertically and sub-vertically (Fig. 10). The hypothetical processes leading to the formation of such rhizosphere traits and ultimately of the bioengineered ferricretes, as suggested by Verboom and Pate (2003, 2006a) have not been demonstrated so far. The exact sequence of events under such aerobic conditions still needs to be elucidated.

Taking account of all of the above-mentioned rhizosphere processes, there is an obvious need to re-examine the impact of higher plants and rhizosphere microbes on the weathering of rocks and minerals for: (1) understanding current rates of weathering and corresponding fluxes in biogeochemical cycles of nutrients (Hobbie 1992) and other elements (e.g., Si, see Lucas et al. 1993; Gérard et al. 2008); and (2) elucidating their role in the biogeochemical history of the Earth, early formation of deep soils in terrestrial ecosystems (pedogenesis) and composition of the atmosphere (CO_2 and O_2 concentrations). These are highly relevant for another major ecosystem service, which is the provision of habitats, because soils are the
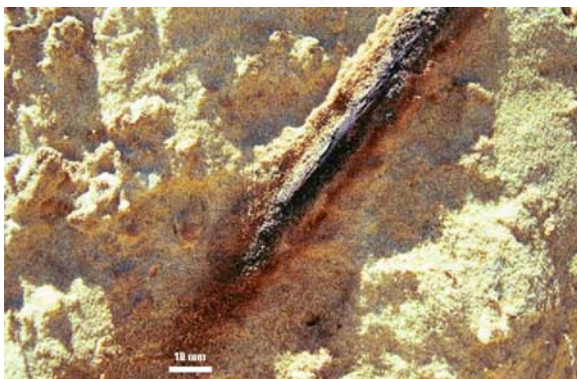
Fig. 10 Biogenic ferricrete around a root of *Eucalyptus* sp. growing vertically, several meters below the soil surface in a deep podzolic soil developed in a sandy parent material at Jandakot, Western Australia. Note iron oxide precipitation in the rhizosphere (photo by Philippe Hinsinger)

greatest reservoir of biodiversity on Earth, and many of the above-mentioned processes have triggered the emergence of this unique diversity (Crawford et al. 2005: Hinsinger et al. 2009). Therefore, higher plants play a central role as drivers of the habitability of the Earth's terrestrial ecosystems (Schwartzman and Volk 1989). *Sensu* Jones et al. (1994), they definitively need to be recognised as key 'ecosystem engineers'.

Concluding remarks

Lovelock (1965) compared the atmosphere of the Earth and other planets, and concluded that living organisms can affect atmospheric composition, finally to their own global benefit. This first idea was then extended to a set of functions that are essential for the development of life at the surface of the Earth. Lovelock considered Earth as a super-organism capable of regulating itself in its own interest. The novelist William Golding poetically called this super-organism Gaia, after the goddess Earth-Mother (Lovelock 2003). Van Breemen (1993) took inspiration from this idea to examine the soils as living constructions (Lovelock 1993). Indeed, soils have been co-constructed by plants and rhizosphere micro-organisms. These have contributed to improving the physical and chemical properties of soils to allow enhanced growth of plants and associated micro-organisms. This has led to increased depth and loosening, structuring, better water retention, better aeration and gas exchange, increased availability of inorganic and organic compounds, enhanced rock weathering and C sequestration. All these properties make the soil a more favourable habitat to sustain the development of living organisms in terrestrial ecosystems. This is certainly linked with the soil being the greatest reservoir of biodiversity on the planet (Crawford et al. 2005). The central and positive role that higher plants have played to improve and maintain the Earth's terrestrial ecosystems in this favourable state, including via a number of rhizosphere processes, needs to be recognised, as stressed by Pate et al. (2001) and Verboom and Pate (2006a). From a global perspective, Schwartzman and Volk (1989) emphasised the role of higher plants in the habitability of Earth. In the current context of global change, it is worth noting that, according to Berner (1992) and Berner and Kothalava (2001), a key

process is the plant-promoted rock weathering, which ultimately allows long-term sequestration of C as carbonate precipitates in the oceans, and thus determines the atmospheric CO_2 concentrations. In that sense, plants and associated microorganisms should be recognised as key 'ecosystem engineers', *sensu* Jones et al. (1994), their major common construction being the rhizosphere.

Major challenges lie ahead of us, to make new discoveries on the signalling processes between the various organisms that play a role in rhizosphere processes. These discoveries will not only enhance our basic understanding, but also allow exciting applications of this new knowledge to deal with pests and diseases in an environmentally responsible manner. There are also major challenges to work towards new crops and cropping systems that are better able to acquire nutrients from soil, in particular P, given that our non-renewable P resources are rapidly running out, with phosphate-fertiliser prices rapidly increasing. Rhizosphere ecology is now a firmly established research field, with many exciting challenges, both from a fundamental and a strategic-applied perspective.

Major developments in our understanding of rhizosphere biogeochemistry and ecology are expected, including greater consideration of long-term temporal scales as well as global scales. Its links with evolutionary processes need to be further understood which is a challenge for the future. While much progress has been made in the case of symbiotic associations, there are considerable knowledge gaps for the many other biological interactions that play a role in the rhizosphere with respect to when and how they have evolved. Answering the puzzling question of why higher plants maintained such a large loss of C via rhizodeposition over tens or hundreds of million years of evolution will be a major challenge. Yet, rhizodeposition is central to many interactions in the soil and to processes beyond rhizosphere ecology. In fact, they are crucial for soil and terrestrial ecosystem functioning and biodiversity.

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