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3.3??Soil?root interface

As a general rule, the surface area of a root system exceeds the leaf canopy it supports. Even disregarding root hairs, the interface between roots of a three-week-old lupin plant and soil is about 100 cm^2 while a four-month-old rye plant under good conditions has more than 200 m^2 of root surface (Dittmer 1937). Trees' root systems are dif?cult to quantify but kilometres of new roots each year generate hundreds of square metres of root surface. Such a root–soil interface arises through the simultaneous activity of up to half a million root meristems in a mature tree.

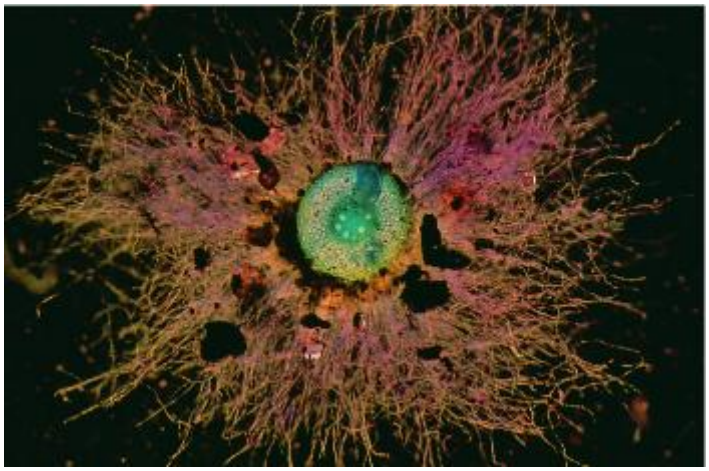

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Figure 3.10 Transverse view of a young, soil-grown wheat root, sectioned by hand and stained with Toluidine Blue. Most soil in the rhizosheath was washed away during preparation, revealing many long root hairs extending from the main axis (diameter 0.6 mm). Root hairs allow this root to explore 21 times more soil volume than would be possible without hairs. A lateral root can be seen extending from the pericycle which surrounds the stele (Photograph courtesy M.Watt)

Many roots form ?ne extensions to epidermal cells called root hairs, amplifying the effective surface area of the soil–root interface many times. Dittmer (1937) estimated that the surface area of root hairs in rye plants was more than that of the root axes on which they grew; similar observations have been made for trees. The aggregate *length* of root hairs in the rye plants studied by Dittmer increased 18 times faster than that of the main axes. Thus, up to 21 times more soil is explored when root hairs are present (Figure 3.10).

Anchorage and extraction of inorganic soil resources both call for a large area of contact between roots

and soil. However, this vast interface is much more than a neutral interface; events within it allow resources to be extracted from the most unyielding soils. Intense chemical and biological activity in a narrow sleeve surrounding roots, particularly young axes, give rise to a *rhizosphere*.

Many root phenomena suggest speci?c roles for the rhizosphere. For example, roots have long been thought to ?nd a relatively frictionless path through soils because of exudation of organic substances and cell sloughing but the chemical and physical processes that underpin this phenomenon are still quite unclear (Bengough and McKenzie 1997). Production of new roots around local zones of enrichment (Section 3.1) is made far more effective through rhizosphere activity associated with these young roots. Phosphate availability is particularly likely to be improved by the presence of a rhizosphere. Potential mechanisms will be discussed below.

Enhancement of root growth under conditions which favour high root:shoot ratios and the attendant rhizosphere surrounding those roots (rhizosheath) require a substantial input of organic carbon from shoots. Some is used in structural roles, while roots and microbes also require large amounts of carbon to sustain respiration. Even in plants growing in nutrient-adequate, moist soils, 30–60% of net photosynthate ?nds its way to roots (Marschner 1995). Carbon allocation to roots can be even greater in poor soils or during drought. The rhizosphere accounts for a large amount of root carbon consumption. Barber and Martin (1976) showed that 7–13% of net photosynthate was released by wheat roots over three weeks under sterile conditions while 18–25% was released when roots were not sterile. This difference might be considered carbon made unavailable for plant growth because of microbially induced demand in the rhizosphere (Section 3.3.3).

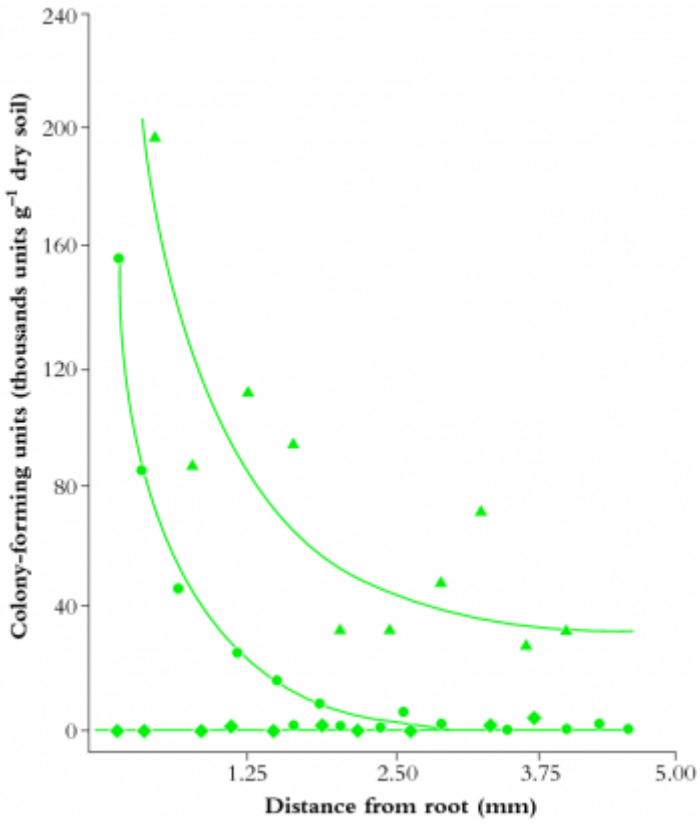

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Figure 3.11 Concentration of *Enterobacter cloacae* (RP8) around wheat roots when the bacterium was introduced by inoculating seeds (circles) or soil (triangles). Uninoculated controls are shown as diamonds. Approximately 3 mm of the

soil around roots supports an elevated bacterial population (Dijkstra *et al.* 1987; reproduced with permission of Elsevier Science)

Rhizosphere chemistry and physics differ from the adjacent soil matrix and root tissues. Gradients in solutes, water and gases combine with microbial activity to produce a unique compartment through which roots perceive bulk soil. This zone of influence extends not more than 3 mm from the root axis (Figure 3.11), partly due to the low diffusion coef?cients of most solutes that move through the rhizosphere (10^{-12} to 10^{-15} m^2 s^{-1} for ions such as orthophosphates). Even a relatively mobile ion such as nitrate, with a diffusion coef?cient (D) of around 10^{-9} m^2 s^{-1} in soil solution, diffuses through about 1 cm of soil in a day. Because the time required (t) for diffusion of ions is a function of the square of distance traversed (l), where $t = l^2/D$ a nitrate ion would take four days to travel 2 cm, nine days to travel 3 cm and so on. Similarly, organic carbon diffuses away from roots only slowly, sustaining a microbial population as it is consumed in the rhizosphere.

Roots advancing through soil perceive a wide range of chemical and biological environments: a rhizosphere simultaneously ful?ls buffering, extraction and defence roles allowing roots to exploit soils. A rhizosphere is thus a dynamic space, responding to biological and environmental conditions and often improving acquisition of soil resources. New roots develop an active rhizosphere which matures rapidly as the root axis differentiates.

3.3.1??Rhizosphere chemistry

Photoassimilate diffuses from roots into the rhizosphere where it is either respired by microorganisms or deposited as organic carbon (‘rhizodeposition’). Some of this photoassimilate loss is in the form of soluble metabolites but polymers and cells sloughed off the root cap also provide carbon substrates. Grasses undergo cortical cell death as a normal developmental process, providing further carbon substrates to support a rhizosphere microflora. Nitrogen and some other inorganic nutrients which are co-released with plant carbon are often reabsorbed by roots. Extraction of minerals from bulk soil also relies strongly on rhizosphere processes, especially near the root apices. Compounds exuded from roots interact with soil components in direct chemical reactions (e.g. adsorption reactions) and through microbially mediated events (e.g. immobilisation reactions). In addition, complex polysaccharides of microbial and root origin give rise to a gelatinous mucilage which associates with soil particles to form a rhizosheath (Section 3.3.3). Rhizosheaths have physical and chemical implications for root function. Hydraulic continuity between soil and roots is, for example, thought to be enhanced by the hydrated mucigel. Negatively charged groups on side-chains of mucilagenous polysaccharides attract cations like Ca^{2+}, providing exchange sites from which roots might absorb nutrients.

Such a diversity of chemical reactions in the rhizosphere is partly an outcome of the array of root-derived compounds. For example, phenolic compounds can be released by root cells in large amounts (Marschner 1995), both as a result of degradation of cell walls and from intracellular compartments. Release of organic acids (principally citric, fumaric and malic acids) solubilises phosphate from surfaces to which they are adsorbed in many species, including those of the family Proteaceae. A modest release of organic acids accounting for about 0.1% of the root mass each week is suf?cient to enhance phosphate acquisition in a selection of annual legumes (Ohwaki and Hirata 1992). In more extreme cases, up to a quarter of the dry weight of *Lupinus albus* plants is released from cluster roots, mostly as citrate (see Case study 3.1). Even the fungal hyphae of mycorrhizal eucalypt and pine roots can secrete photoassimilates, in the form of oxalic acid, causing phosphorus to be solubilised from

insoluble calcium apatite (Malajczuk and Cromack 1982).

The main families of low molecular weight compounds which react with inorganic ions are phenolics, amino acids and organic acids. Heavy metals such as aluminium, cadmium and lead are complexed by phenolics, affecting the mobility and fate of these ions in contaminated soils. Manganese is complexed by organic acids, as are ferric ions, which also interact chemically with phenolic compounds and amino acids. For example, highly specialised amino acids (phytosiderophores) can complex ferric ions and enhance uptake from soils by rendering iron soluble. Low iron status actually stimulates release of phytosiderophores into the rhizosphere (Marschner 1995). Other metals such as zinc and copper might also be made more available to the plant through the chelating action of phytosiderophores. Chemical processing by chelating agents is dependent on plant perception of nutrient de?ciencies, leading to an ordered change in rhizosphere chemistry. A signi?cant demand on photoassimilates is required to sustain chelation of nutrient ions.

Enzymes are also released from roots, particularly phosphatases, which cleave inorganic phosphate from organic sources. The low mobility of orthophosphates means that phosphatases can be an important agent in phosphorus acquisition, especially in heathland soils where the native phosphorus levels are low relative to the phosphorus-rich remnants of decaying plant material.

pH is another important rhizosphere property. Roots can acidify the rhizosphere by up to two pH units compared to the surrounding bulk soil through release of protons, bicarbonate, organic acids and CO_2. In contrast, the rhizosphere of roots fed predominantly with nitrate was more alkaline than bulk soil. A distinct rhizospheric pH arises because of the thin layer of intense biological activity close to roots, especially young roots. In addition to proton fluxes, release of CO_2 by respiring roots and microbes is likely to cause stronger acidi?cation of the rhizosphere near root apices where respiration is most rapid.

Rhizosphere acidi?cation affects nutrient acquisition by liberating cations from negative adsorption sites on clay surfaces and solubilising phosphate from phosphate-?xing soils. Furthermore, micronutrients present as hydroxides can be released at low pH, conferring alkalinity tolerance on those species with more acidic rhizospheres. So, the rhizosphere is a space which ensheathes particularly the youngest, most active parts of a root in a chemical milieu of the root’s making. In this way, acquisition of soil resources is strongly controlled by processes within roots. Local variations within soil are buffered by rhizosphere chemistry, enabling roots to exploit heterogeneous soils effectively.

3.3.2??Rhizosphere biology

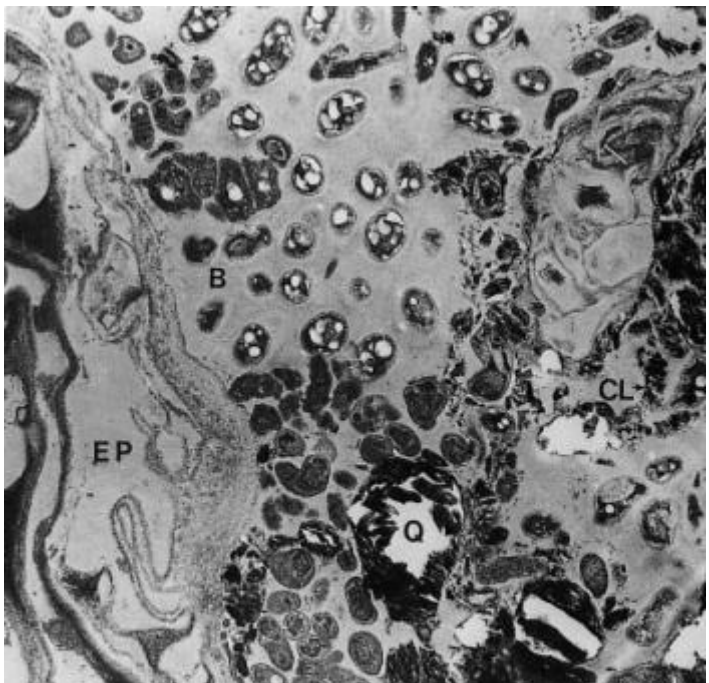

Figure 3.12 Mature rhizosphere from roots of clover (*Trifolium subterraneum* L.). The outer cortex has been crushed and epidermal cells (EP) have become distorted, leading to leakage of substrates into the rhizosphere. The rhizosphere is rich in microorganisms with bacteria (B) clearly visible. Soil (Q) and clay (CL) particles are held together in the inner rhizosphere by a mucilage of polysaccharides. Sustained losses of carbon required to maintain this microflora are thought to come from exudation and senescence of root cells. (× 10 000) (Foster *et al.* 1983; reproduced with permission of Springer-Verlag)

Microbial activity, sustained by photoassimilates secreted from roots, contributes substantially to rhizosphere properties. The level of microbial activity is also influenced by availability of nitrogen as a substrate for microbial growth. Soils with high fertility and biological activity have microbial densities 5–50 times greater in the rhizosphere than in bulk soil. The diversity of rhizosphere microflora is spectacular (Figure 3.12) and still incompletely described. Early studies in South Australia showed that *Pseudomonas* and *Arthrobacter* species are present on roots in ratios which reflect the rapid doubling times and competitive dominance of *Pseudomonas* (Bowen and Rovira 1976). Within genera, species of *Pseudomonas* have frequencies varying up to 500-fold. In general, gram-negative bacteria, fungi and ascomycetes (Section 3.4) are most abundant.

Rhizosphere microorganisms are not uniformly distributed along roots. Apices are almost free of microbes but densities can increase dramatically in subapical zones. Very mature root axes with lateral branches are sparsely populated with microbes. In maize roots, the area occupied by microorganisms is only 4% nearest the root apex, rising to 20% in subapical zones (Schönwitz and Ziegler 1986). Even within these zones, there are large variations in distribution, with radial epidermal walls of roots secreting exudates which can support huge microbial populations, up to 2×10^{11} microbes cm^{-3}.

Roots do of course influence adjacent soil throughout their length by setting up gradients of water, gases and ions. For example, in waterlogged soils leakage of O_2 from aerenchymatous roots leads to oxidation of metal ions and local build up of aerobic microflora around roots of agricultural plants (Chapter 18). In general, however, the most active microbial populations and rates of chemical transformation in the rhizosphere occur in the subapical zones of the root. In supporting these processes, root-associated microbes metabolise inorganic nitrogen, depositing protein nitrogen in the process of immobilisation. Microbial activity also produces plant growth regulators such as auxin, cytokinins and gibberellins, possibly in amounts suf?cient to influence root morphogenesis. Ethylene can also be produced by rhizospheric fungi, potentially influencing root morphological changes such as lateral root initiation.

3.3.3??Costs and bene?ts of a rhizosphere

Root function and overall plant performance can bene?t conspicuously from processes in the rhizosphere. Infection by rhizobia (Section 3.5) and mycorrhizal fungi (Section 3.4) improve the nutritional status of many species and rhizobial strains have even been used to manipulate rhizosphere biology. Under natural conditions, intense microbial competition occurs in the rhizosphere, as seen by the success of *Pseudomonas* spp. discussed in Section 3.3.2, but the variability of soils, plant species and environmental conditions make it impossible to predict rhizosphere composition.

A signi?cant proportion of photoassimilate is used to support a rhizosphere, reflecting the high cost of microbial activity and polymer exudation. This pattern is repeated in many species with up to 20% of plant carbon consistently lost by roots. Relative rates of microbial and root respiration are almost impossible to estimate in roots growing in undisturbed soils because of the intimacy of roots and microbes. In addition to consuming large amounts of plant carbon, microbes produce phytotoxins which can impose further restrictions on root function.

Mechanisms describing how a rhizosphere *bene?ts* its host are even more elusive because of the diversity of reactions in such a small space. Chelation is identi?ed as a major influence on nutrient acquisition and might also help ameliorate ion toxicities. Physical properties of the rhizosphere are even less well understood, with questions such as root lubrication, root–mucilage shrinkage and interfacial water transport not yet resolved. Limited data do not support earlier notions of mucilage as a water-holding matrix and while secretions might help roots advance through soil, most friction is thought to be between root axes and cap cells (Bengough and McKenzie 1997). Physical properties of mucilage do not suggest it is an ideal lubricant. Whether the dynamic properties of a rhizosphere bring constant bene?ts to a plant or simply passively coexist with growing roots remains a critical question.

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