A history of rhizosphere research – roots to a solution

Peter J. Gregory

SCRI (Scottish Crop Research Institute), Invergowrie, Dundee, DD2 5DA, UK, Email peter.gregory@scri.ac.uk

Abstract

The availability and accessibility of water and nutrients to plants, and the interactions of roots with soil, continue to be subjects of active research. Hiltner's insight that there was a volume of soil, the rhizosphere, over which the roots had influence, and in which a range of processes occurred, was a major advance in thinking. Soil science, though, took some time to incorporate this notion into its mainstream thinking. Nutrient and water availability to plants was defined throughout the early 1900s in equilibrium terms; for nutrients with chemical extractants, and for water by the equilibrium concepts of field capacity and permanent wilting point. It was not until the mid 1950s that ideas of water and nutrient mobility superseded ideas of thermodynamics and equilibria with measurements of convective and diffusive movement of resources to roots demonstrating the size of the zone of root influence. The size of the rhizosphere differs spatially and temporally depending on the resource considered, with microorganisms experiencing strong gradients. For the future, while direct management of rhizosphere properties to enhance the efficiency of N fixation is already a reality, interventions that will improve the recovery of nutrients and other resources are still a major challenge.

Key Words

Root systems, microorganisms, rhizodeposits, aggregation, phytase, root elongation.

Introduction

The concept of the rhizosphere originated with Hiltner's (1904) field and pot studies of the effects of green manuring with legumes on soil fertility. He determined that, to explain his observations, there must be a series of processes occurring at the root/soil interface. Among the processes occurring, it was clear that: i) a volume of soil existed that was shared by roots and bacteria; ii) exuded materials from the roots of different legumes attracted different organisms than roots of non-legumes; and iii) each legume species attracted organisms that had a specific benefit for that species. His main insight from these observations was that there was a volume of soil, the rhizosphere, over which the roots had influence and that this soil volume was also shared by bacteria. Apart from a few soil microbiologists, though, soil scientists in general took some time to incorporate this concept into their mainstream thinking.

As Gregory (2006) relates, the role of roots in determining plant accessibility to water and nutrients received little attention throughout the early 1900s when availability of nutrients to plants was defined by use of chemical extractants and that of water was similarly defined by the equilibrium concepts of field capacity and permanent wilting point. It was not until the mid 1950s that ideas of water and nutrient mobility superseded those of equilibria and thermodynamics. For nutrients, the change of thinking came in a ground-breaking paper by Bray (1954) in which he introduced the concept that nutrient mobility was central to soil-plant relations, and demonstrated that mobile nutrients such as nitrate moved to roots from large distances whereas adsorbed nutrients such as phosphate moved only short distances. The corollary of this was that the zones of competition for nutrients by roots differed depending upon the mobility of the nutrient. This change of thinking about the availability of nutrients to plants was paralleled by similar developments regarding the movement of water towards roots (Gardner 1960).

Besides a few contributions to mainly biological journals, neither roots nor the rhizosphere impinged on the soil science literature as topics of major importance until the latter part of the 1900s. Gregory (2006) showed in a survey of the major soil science journals at five-year intervals from 1950 onwards that roots or the rhizosphere featured in only a very small number of papers until about 1990. The major soil science journals still carry few such papers (Soil Biology and Biochemistry excepted) and Plant and Soil has emerged as the journal carrying the most papers on the plant/soil interface, with substantial coverage also in New Phytologist.

Recent understanding of the rhizosphere

The rhizosphere is a "zone of soil surrounding the root which is affected by it" (Darrah 1993) but its size differs spatially and temporally depending on the factor considered, ranging from a fraction of a mm for

microbial populations and immobile nutrients to tens of mm for mobile nutrients and water to several tens of mm for volatile compounds and gases released from roots. This means that the interface between the root and the soil is complex, frequently an ill-defined boundary, and heterogeneous in space and time. Compounds released from roots into the soil change its chemical and physical properties, and stimulate the growth of various organisms. Rhizodeposits of various exudates, sloughed cells and decaying roots provide an important substrate for the soil microbial community and there is a complex interplay between this community and the quantity and type of compounds released (Marschner and Baumann 2003). There is increasing evidence that microorganisms (particularly rhizobia) can alter processes within plant roots especially those related to root hair and lateral root development (e.g. Mathesius 2008). Much research has now demonstrated that other compounds released from roots may act as messengers that communicate and initiate root-root, root-microbe, and root-faunal interactions (Walker *et al*. 2003). Root-microbe and root-insect interactions can be either positive (symbiotic) to the plant (e.g. via associations with mycorrhizal fungi and N-fixing bacteria) or negative to the plant (e.g. interactions with parasitic plants, pathogenic microbes and herbivorous insects).

Chemical changes in the rhizosphere of plants have been widely reported (see Hinsinger *et al*. 2009 for a review), though their quantitative significance for crops is still a matter of debate. Depletion of nutrients such as N, P and K close to roots is widespread, while others such as Ca, Mg and S may accumulate depending on soil solution concentrations, plant demand and transpiration rate. In addition to changes in ionic concentrations of nutrients, there are four other major root-induced changes to the chemical environment of the rhizosphere mediated through alterations of: i) pH; ii) reduction/oxidation conditions; iii) complexation of metals; and iv) enzyme activities. In particular, the release of organic anions such as malate and citrate by roots can offset the toxic effects of aluminium as well as acting to solubilise P (Kirk *et al*. 1999; Ryan *et al*. 2009)

Physical changes in the rhizosphere have been much less studied than biological or chemical changes, despite their potential consequences for the movement of water and solutes. The release of root mucilage may change the water relations of the rhizosphere. For example, Read *et al*. (2003) showed that the addition of the surfactant component of mucilage can alter the relationship between water content and soil matric potential (the moisture characteristic curve) making the soil drier at a given value of matric potential, especially at high matric potentials. Whalley *et al*. (2005) also found that rhizosphere soil of maize and barley tended to be drier at a given matric potential than bulk soil but suggested that differences in wetting angle and pore connectivity were the likely explanation for these differences. The development of water-stable aggregates is an important process in the genesis of soils because it strongly influences a range of soil characteristics including aeration, infiltration and erodability. Plant roots play a major role in this process. Their influence comes about indirectly through the release of carbon compounds which provide a substrate for microbes (Young and Crawford 2004), and directly through: (i) wetting and drying phenomena; (ii) the accumulation in some soils of inorganic chemicals at the root surface that act as cementing agents; (iii) the release of organic compounds that promote aggregation of particles; and (iv) the structural support of undecayed, senescent roots which act like steel rods in reinforced concrete.

The future – solutions to crop production constraints
With the development of new imaging techniques, genetic manipulation of roots and the development of process-based models, the future for rhizosphere exploration appears bright and will, in time, lead to practical ways of controlling performance in the field. Three areas that where progress is starting include:

Utilisation of genes to modify root surface properties
Near isogenic lines are already available to study aspects of root growth such as the effect of dwarfing and semi-dwarfing genes on root growth (e.g.Wojciechowski *et al*. 2009) and transgenic plants able to excrete specific enzymes will open up aspects that are currently difficult to explore. For example, George *et al*. (2009) demonstrated that for tobacco plants transformed to exude phytase, the presence of rhizosphere microorganisms reduced the dependence of the plants for extracellular secretion of phytase from roots when grown in a P-deficient soil. However, the expression of phytase in transgenic plants had little or no impact on the microbial community structure as compared to control plant lines, whereas soil treatments, such as addition of inorganic P, had large effects. The results demonstrated that soil microorganisms are explicitly involved in the availability of P to plants but that the microbial community in the rhizosphere appears to be resistant to single-gene changes in plants designed to alter rhizosphere biochemistry and nutrient cycling.

Managing rhizosphere biophysics
Soil strength at the root apex affects both the pressure that a root must exert to penetrate the soil and the

degree of colonisation by soil microorganisms (Hinsinger *et al*. 2009). Mucilage and root cap cells lubricate the passage of the root through soil (Iijima *et al*. 2004) but the ability of some roots to continue growth at strengths that inhibit shoot growth and/or root growth in other species is an important property that might be amenable to genetic manipulation. For example, Clark *et al*. (2000) used wax layers to screen the differential ability of six rice genotypes to penetrate strong soils and found substantial differences in the number of axes penetrating the layer. Further research is necessary to determine the genetic factors influencing both the production of lubricants and the underlying factors influencing root growth in hard soils.

Quantification of complex, interacting processes using mathematical models
Many studies of rhizosphere processes have indicated the presence or absence of a process in particular circumstances but many processes may operate in parallel. For example, plant P acquisition from a soil with low plant available P may depend on production of root hairs, degree of mycorrhizal infection and efficacy of the fungus, changes in soil pH, release of organic anions, changes in redox potential, release of enzymes etc. These processes often interact and measuring them in experimental systems is difficult although their end result can be determined. Mathematical models can assist in assessing the contribution that each process makes to the final result and in indicating which processes are important in various circumstances. In upland rice, for example, modelling demonstrated that the measured P uptake of the plants was a consequence of P solubilization by organic anions principally through the chelation of metal ions that would otherwise have immobilized P or through the formation of soluble citrate-metal-P complexes or both, whereas displacement of P from adsorption sites was unimportant (Kirk *et al*. 1999).

References

Bray RH (1954) A nutrient mobility concept of soil-plant relationships. *Soil Science* **78,** 9-22.
Clark LJ, Aphalé SL, Barraclough PB (2000) Screening the ability of rice roots to overcome the mechanical impedance of wax layers: importance of test conditions and measurement criteria. *Plant and Soil* **219,** 187-196.
Darrah PR (1993) The rhizosphere and plant nutrition: a quantitative approach. *Plant and Soil* **155/156,** 3-22.
Gardner WR (1960) Dynamic aspects of water availability to plants. *Soil Science* **89,** 63-73.
George TS, Richardson AE, Li SS, Gregory PJ, Daniell TJ (2009) Extracellular release of a heterologous phytase from roots of transgenic plants: does manipulation of rhizosphere biochemistry impact microbial community structure? FEMS (in press)
Gregory PJ (2006) Roots, rhizosphere and soil: the route to a better understanding of soil science? *European Journal of Soil Science* **57,** 2-12.
Hiltner L (1904) Über neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter besonderer Berücksichtigung der Gründüngung und Brache. *Arbeiten der Deutschen Landwirtschaftlichen Gesellschaft* **98,** 59-78.
Hinsinger P, Bengough AG, Vetterlein D, Young IM (2009) Rhizosphere: biophysics, biogeochemistry and ecological relevance. *Plant and Soil* **321,** 117-152.
Iijima M, Higuchi T, Barlow PW (2004) Contribution of root cap mucilage and presence of an intact root cap in maize *(Zea mays)* to the reduction of soil mechanical impedance. *Annals of Botany* **94,** 473-477.
Kirk GJD, Santos EE, Santos MB (1999) Phosphate solubilization by organic anion excretion from rice growing in aerobic soil: rates of excretion and decomposition, effects on rhizosphere pH and effects on phosphate solubility and uptake. *New Phytologist* 142, 185-200.
Marschner P, Baumann K (2003) Changes in bacterial community structure induced by mycorrhizal colonisation in split-root maize. *Plant and Soil* **251,** 279-289.
Mathesius U (2008) Auxin: at the root of nodule development? *Functional Plant Biology* **35,** 651-668.
Read DB, Bengough AG, Gregory PJ, Crawford JW, Robinson D, Scrimgeour CM, Young IM, Zhang K, Zhang X (2003) Plant roots release phospholipid surfactants that modify the physical and chemical properties of soil. *New Phytologist* **157,** 315-326.
Walker TS, Bais HP, Grotewold E, Vivanco JM (2003) Root exudation and rhizosphere biology. *Plant Physiology* **132,** 44-51.
Whalley WR, Riseley B, Leeds-Harrison PB, Bird NRA, Leech PK, Adderley WP (2005) Structural differences between bulk and rhizosphere soil. *European Journal of Soil Science* **56,** 353-360.
Wojciechowski T, Gooding MJ, Ramsay L, Gregory PJ (2009) The effects of dwarfing alleles on seedling root growth of wheat. *Journal of Experimental Botany* **60,** 2565-2573.
Young IM, Crawford JW (2004) Interactions and self-organization in the soil-microbe complex. *Science* 304, 1634-1637.