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REVIEW

Biophysical interactions at the root–soil interface: a review

I. M. YOUNG*

Soil–Plant Dynamics Unit, Scottish Crop Research Institute, Dundee DD2 5DA, UK

INTRODUCTION

Soil close to roots generally has chemical, physical and biological properties which are significantly different from those of soil located some distance away (Jenny & Grossenbacher 1963; Hawes & Pueppke 1986; Young 1995). The root–soil interface is defined as soil near to or adhered to the root surface to some small distance into the soil matrix. This distance may vary between < 1 mm and *c.* 10 mm. Working definitions include rhizosphere, where 'zones of influence' are inferred, and rhizosheath, when soil adhered to the root is discussed. Most work carried out at the root–soil interface has concentrated on biological or chemical processes, due both to the fact that the relevant techniques required to examine these processes have been more advanced than the physical techniques, and also because the farmer is generally offered either biological or chemical solutions to his everyday problems, as these are readily accessible, easy to use and cheap. The main manipulation of soil physical conditions occurs during cultivations, and the addition or removal of water from the soil profile. Intensive cultivations are a regular occurrence in many farming systems, despite the potential drawbacks: damage of the soil structure, leading to reduced crop yields and an increased risk of erosion.

The main aim of this review is not to cover all the complex issues related to the root–soil interface. Instead, it concentrates on the biophysical processes which, compared with conventional plant physiological and soil microbiological research, have attracted relatively limited attention (e.g. see Waisel *et al.* 1996). The review examines small-scale (μm-mm) interactions and, where possible, links their impact to the larger scale. Three interacting areas are investigated: the physical structure of the soil and root growth, water dynamics and microbial dynamics.

The dynamics of structural change and root growth

All soil processes occur in a heterogeneous structural framework, connected by a 3-D multi-scaled network of tortuous pores. The heterogeneity acts to separate microbial communities, carbon substrates and roots spatially. There is a two-way interaction between soil structure and biota in that biota may act to alter the geometry of the structure through which they operate, which ultimately modifies the future functioning of the biota and the structure. At the scale of the individual root, and smaller, the main controlling mechanisms of such structural changes are microbes (Foster 1988), fauna (Blanchart *et al.* 1993) and the roots themselves (Reid & Goss 1981). The role of the roots in altering soil structural characteristics significantly is, however, contentious. Theoretically, an expanding root exerts radial (side) and axial (forward) pressures into the soil (Misra *et al.* 1986). Consequently, the soil should be denser around and in front of the growing root. Clearly, increasing density at the root-tip would be self-defeating, as there is an inverse relation between soil bulk density and root elongation rate (Bengough & Mullins 1990). However, radial expansion by the root is thought to create tensile stresses, and thus cracks, in front of the root tip, reducing the energy the root has to expend in elongation (Hettiaratchi 1990). This is an effective strategy to adopt as the ratio of compressive to tensile strength is *c.* 8, depending on the soil matric potential (Young & Mullins 1991). Therefore it is energetically cheaper for the root to fail the soil by creating cracks than by any other method.

Nye & Tinker (1977) discount increases in soil density due to root growth as having any significance over solute fluxes to the root. Based on the results of Greacen *et al.* (1968) and Cockroft *et al.* (1969), this conclusion is probably correct. These results show that roots increase soil dry bulk densities by *c.* 5%. Yet Dexter (1987) developed a model that predicts exponential decreases in density with distance from the root–soil interface within a homogeneous soil, and more recent experimental work backs up this model. Using a radiograph technique, Braunack & Freebairn (1988) examined the effects of elongating pea, wheat and maize roots on subsequent soil density changes around roots. Compared with the initial

* Email: imy@scri.sari.ac.uk

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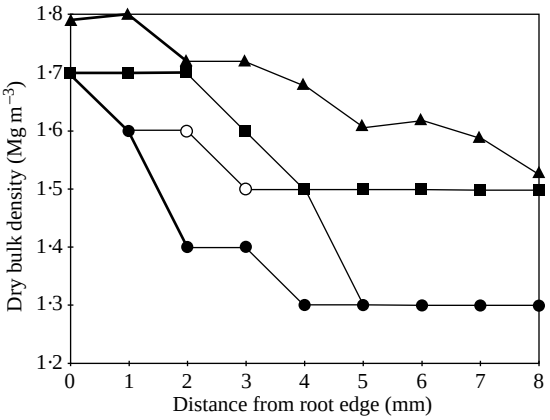


Fig. 1. Changes in soil dry bulk density (Mg m^{-3}) around the root caused by root elongation: Braunack & Freebairn (pea), ●; Braunack & Freebairn (wheat), ■; Braunack & Freebairn (maize), ○; Bruand *et al.* (maize), ▲. See text for details of references.

packing densities, roots of all species increased the soil density by 36% at the root edge. Based on absolute values, these results show increases from initial densities of 1·25 Mg m^{-3} to 1·7 Mg m^{-3}, at the root–soil interface. At 3 mm from the root, densities increased by 12, 28 and 20% for pea, wheat and maize, respectively; and at 8 mm, 4, 20 and 20% increases were observed. These data are supported by Guidi *et al.* (1985) who, using mercury intrusion porosimetry, found, on average, total porosity decreasing from 0·171 in bulk soil aggregates to 0·141 in root–soil aggregates (representing a 17% increase in density). A note of caution should be expressed concerning the results of Guidi *et al.* (1985). Back calculation of absolute values of density (the original data are expressed as total porosity) yields, assuming a particle density of 2·65 Mg m^{-3}, a dry bulk density of 2·28 Mg m^{-3}. This figure is unrealistically high: typical values are in the range 1·1–1·7 Mg m^{-3} in the field (Young *et al.* 1991). Whatever the reason for this discrepancy, however, the *relative* increases in density are probably correct. Additional information concerning the effect of a growing plant on soil density comes from Liddell (1992) who examined alterations in dry bulk density around emerging wheat coleoptiles. The maximum density value (1·3 Mg m^{-3}) was observed near the edge of the shoots, representing an increase of 35%.

The data presented above were all obtained by using sieved soil. However, recently Bruand *et al.* (1996) have investigated the changes in porosity around maize roots with thin sections taken from undisturbed cores of a fine-loamy soil. Using back-scattered electron scanning, their results support the claims made by previous workers, showing that the bulk density of soil surrounding the root increased up to 1·80 Mg m^{-3}, from an initial density of 1·54 Mg m^{-3}: representing an increase of 17%. Furthermore, the data presented by Bruand *et al.* (1996) have a good fit to the Dexter (1987) model. A graphical summary of the root data is shown in Fig. 1.

It is not clear whether localized increases in density are found consistently in field soils and, as such, it is difficult to attribute more than potential effects of localized structural change on soil processes. The propensity for a root to alter density will be root- and soil-specific (Braunack & Freebairn 1988). The heterogeneous nature of soil structure limits the consistency we can expect, and clearly root–soil contact may change dramatically down a single root (van Noordwijk *et al.* 1992), affecting not only possible density changes but also rates of water uptake. Additionally, alterations in the soil structure bring associated changes in water regimes (Hall *et al.* 1977), gas diffusion (Nye & Tinker 1977) and, in the rhizosphere, generally large increases in microbial dynamics. Clearly, large and significant increases in density can occur solely due to roots elongating in the profile, absolute values of which are comparable to tractor-induced compaction, on a larger scale.

Aspects of structural dynamics in the rhizosphere with respect to local root-induced density changes have impact in a number of areas. Gilligan (1979) proposed a model predicting the probability of soil-borne pathogen attack based on the size of the rhizosphere and the distance of pathogens from roots. Gilligan & Bailey (1997) developed a similar but more sophisticated model which, in part, takes account of local density changes around roots. Gilligan (1985) used the term 'pathozone', rather than rhizosphere, to emphasise the volume of soil surrounding the root within which a pathogen must be present. In very general terms, the probability of infection of a root by a pathogen decreases as the distance from the pathogen to the root increases. Any increase in density around the root (by whatever mechanism) may act to decrease the pathogen–root distance and hence increase the probability of infection. The early models and approaches related to microbial movement towards roots originally dealt with relatively simple soil volume elements (Gilligan 1979; Ferriss 1981) but have since advanced to take account of the variability of micro- and meso-scale structural and water dynamics (Grose *et al.* 1996; Anderson *et al.* 1997).

In the case of structure–biota interactions at the root–soil interface, it is always true that structural heterogeneity and water distribution act in tandem. The ease with which microbes can move within or towards the rhizosphere relies on hydraulic pore connectivities which may be only a small fraction of the total pore connectivity and certainly a small portion of the total soil porosity. In practical terms, the problem of incorporating structural elements into

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soil process models has been how to observe, quantify and model these elements. However, to some extent, this is now being achieved. Anderson *et al.* (1997) apply a cellular automata theory to examine the effects of structural parameters, including local density changes, on nematode movement towards roots. Grose *et al.* (1996) employ X-ray computer tomography to identify moisture patches around wheat roots with respect to fungal pathogen attack. Whilst these approaches do have some drawbacks, they have significantly advanced the incorporation of structural elements into microbial models, recognising that the physical habitat of the soil plays a fundamental role in defining and mediating the rate and degree of all soil microbial processes. This is a crucial step forward. Until recently, most models dealing with microbial activity dealt with relatively simplistic biological systems operating in generally structureless media (Darrah 1991; Bazin & Prosser 1992; Focht 1992). The dynamics of biological parameters must be examined in the context of their habitat. This is a well-known principle in ecological studies (Odum 1969), and must now be emphasised in soil research.

Water at the root–soil interface

There has been a large body of literature analysing and interpreting water uptake by roots (Monteith 1986; Passioura 1988). The general image over time is of soil matric potential decreasing near the root; the soil becomes drier closer to the root. Nuclear magnetic resonance (NMR) images examined by MacFall *et al.* (1991) show that there may be significant heterogeneity in water uptake as evidenced from cross-sections of pine roots growing in sand. One of the main features, not commented on in any detail by MacFall *et al.* (1991), is the increasing heterogeneity of uptake seen over time. In some cases, one side of the pine root depletes water to some distance into the sand whilst, on the other side, depletion is limited to close to the root. This could be due to some combination of (i) heterogeneity of sand structures, (ii) different water uptake characteristics in a single root, or (iii) different water status at either side of the root. It is not clear which reason contributes most to the results. What is clear is the remarkable heterogeneity in water depletion around one root.

Moisture conditions close to the root control the activity of rhizosphere micro-organisms (Parke *et al.* 1986), the potential for pathogen attack (Grose *et al.* 1996) and the hydraulic conductivity for water flow into the root (Passioura 1988). Several workers have examined the nature and origin of heterogeneity in water uptake and how this affects the moisture conditions in the rhizosphere. The rate of water uptake is defined by the transpiration rate and the resistance to water flow in the soil and in the root. McCully & Canny (1989) investigated the effect of variable resistance to water flow through maize root metaxylem vessels and Wang *et al.* (1991) examined how such resistances influenced the moisture conditions around the root. McCully & Canny (1989) observed that where soil was adhering tightly to the root (the rhizosheath), small (*c.* 20 μm diameter) early metaxylem vessels controlled water uptake into the root. Where soil did not adhere to the root, larger (*c.* 100 μm diameter) late metaxylem vessels controlled water flow. As the rate of flow is directly proportional to fourth power of the radius, each late metaxylem vessel would carry 625 times the volume of water of an early metaxylem vessel. Thus, most of the water flow from soil to root would have occurred away from the rhizosheath. Logically then, the rhizosheath soil should be wetter than the non-rhizosheath soil (Wang *et al.* 1991). However, no direct quantitative evidence exists linking water uptake by metaxylem vessels to moisture patchiness around the root. Yet, such patchiness can, and does, occur, temporarily reversing the expected soil moisture gradient and leading to relatively wet rhizosheath soil (Young 1995). The phenomenon of reverse flow of water from roots to soil is well documented (Bormann 1957; Molz & Peterson 1976) and may be one source of wet rhizospheres. The term 'hydraulic lift' has been adopted to describe the transfer of water from deep wet soil through the root system to drier topsoil, under low light intensities. At some point the rhizosphere soil would be wetter than soil some distance from the root, due to the efflux of water from the root. Typically, hydraulic lift is thought to occur mostly in arid or semi-arid environments (Richards & Caldwell 1987), although recently it has been observed in more mesic environments during periods of drought (Dawson 1993). Baker & van Bavel (1986) observed hydraulic lift across relatively large matric gradients ($-0{\cdot}002$ to -10 MPa), whilst Vetterlein & Marschner (1993) observed water moving from roots into soil when the soil matric potential dropped below only -10 kPa, showing that, during the night, 10·8 ml water was released into the top 10 cm of the soil profile by roots. The question is, can plants use 'hydraulic lift' as a strategy to overcome water or nutrient deficiency?

Dawson (1993) examined the magnitude of hydraulic lift for sugar maple (*Acer saccharum*) and the effects of such a transfer of water on the surrounding shallower rooted plants. Using stable hydrogen isotope analysis, Dawson (1993) demonstrated that all the shallow-rooted plants close to the maples (up to 3 m away) were able to access a significant portion of the water transferred by the maple's root system by hydraulic lift. The portion used varied between 3 and 60% and, under drought conditions, significantly decreased the water stress experienced by the surrounding vegetation. Furthermore, as the proportion of the hydraulic lift water used by the shallow-rooted

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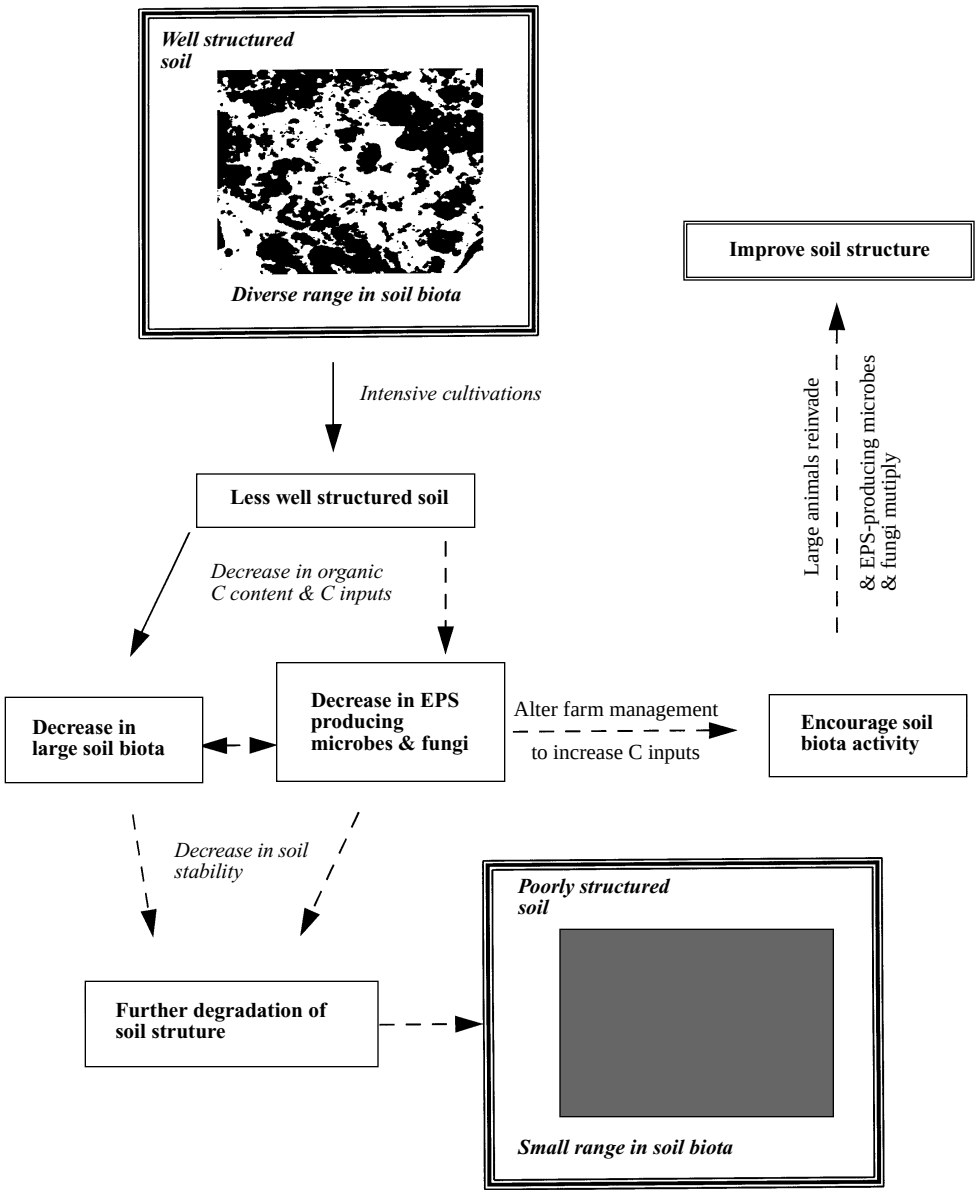


Fig. 2. A proposed model to investigate the interactions of soil structure and biota over a range in scales.

plants increased, so did their above-ground growth. Caldwell & Manwaring (1994) examined the effect of hydraulic lift in reducing the spatial soil nutrient heterogeneity using a shrub (*Artemisia tridentata* ssp. *vaseyana*). The idea was that where hydraulic lift was operating, less heterogeneity would be observed in the soil's ability to supply the plant with a range of nutrients, as a result of increased water supply and the resultant increased hydraulic and nutrient conductivity between root and soil. However, no such correlations were observed. Although hydraulic lift could potentially influence a number of important soil–plant–microbe processes by transferring water around the soil profile, bypassing the soil pore pathways, it has as yet only been shown to be of significance for plant water uptake.

Microbes and mucilage at the root–soil interface

Mucilage secreted by roots has undoubted biological (Rougier & Chaboud 1985) and nutritional (Uren & Reisenauer 1988) significance. There are three main

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areas where the impact of root-exuded mucilage is being implicated in soil biophysical processes: aggregate stability, water-holding capacity (Chenu 1993) and diffusion in the soil (Anderson *et al.* 1997). Aggregate stability relations will be examined here.

The dynamics of mucilage and microbes in the soil affect soil structural stability either by 'gluing' particles together and/or by stimulating microbial activity (Tisdall *et al.* 1978). At the scale of the rhizosphere, the main source of carbon is through exudation at various points along a root, and the release of extra-cellular polysaccharides (EPS) by rhizosphere bacteria. Morel *et al.* (1991) added maize root exudate to a silt loam soil, resulting in a rapid 40% increase in stable aggregates. After 21 days incubation, however, stability decreased to that of the control. Similar trends were found for a silty clay, although after similar incubations significantly higher stabilities (*c.* 5%) were maintained, compared to the control. In a study related to rhizosheath formation, Watt *et al.* (1994) found that initially drier soil conditions enhanced the cohesiveness of rhizosheath mucilage and stimulated root hair production. As a result, the stability of the rhizosheath soil was 40% greater in initially dry, compared to initially wet, soil. McCully (1995) suggests that the nocturnal efflux of water allows the expansion of root-cap mucilage into soil. Once drying occurs, when transpiration starts, the mucilage binds tightly to the soil, thus stabilizing it. McCully & Boyer (1997) suggest that the action of the mucilage on soil during the drying periods may cause local increases in soil density at the root–soil interface. However, no quantitative evidence is provided, and a retreating water meniscus may be all that is required to create some shrinkage of soil around the root.

Roberson *et al.* (1991) and Edgerton *et al.* (1995) have observed linear relations between aggregate stability and microbial biomass, in agricultural and restored soil, respectively. However, it has also been shown that the addition of C to soil may decrease soil stability (Reid & Goss 1981; Reid *et al.* 1982). Such reductions depend on the digestibility of carbon substrates by micro-organisms and the ease with which carbon is absorbed and physically and/or chemically protected in soil (Chenu 1993).

The dynamics of mucilage and microbes which operate on a small scale, particularly in the rhizosphere, have clear and significant impacts on a large scale and are of significance to the farmer. Roberson *et al.* (1995) manipulated the C:N ratios of inputs into soil and examined EPS production and soil aggregation. They found that N availability controlled EPS production and, in high N plots, saturated hydraulic conductivity, aggregate slaking resistance and high fraction (HF) carbohydrate contents were significantly lower than in lower N plots. HF carbohydrate was rich in EPS. The improvements in soil structural stability and changes in water flow characteristics were all achieved without a significant reduction in tomato crop yields.

The link between soil micro-organisms and soil structure is two-way. All biota can alter the physical framework of the soil either by disturbing the structure or by changing it indirectly by exuding gluing agents and C substrates. This in turn acts to modify the movement and dynamics of the micro-organisms themselves, by altering pore pathways and water dynamics (Chenu 1993). Figure 2 presents a number of interlinked processes relevant to these interactions, attempting to link the small-scale processes with large-scale events, and vice versa. Whilst some of the links are known, many have not been examined and warrant attention. At present, farmers do little to manipulate soil micro-organisms directly. With the increase in the amount of waste (and thus carbon inputs) being applied to land, opportunities to exploit soil structure–biota interactions exist, with short-term benefits to the farmer and long-term benefits to the environment. To succeed, research has to be co-ordinated and integrated across disciplines, and set within testable hypotheses, some of which are outlined in Fig. 2.

CONCLUSIONS

This brief review has concentrated on research linking soil structure, water and microbial movement at or near the root–soil interface. The running theme has been heterogeneity; its origin and how it may affect soil–plant interactions. From a number of research areas, it is clear that the biophysical processes occurring on a small scale can impact on a wide variety of soil processes which are of immediate concern to farmers: such as the stability of soil, plant water uptake and pathogen movement towards plants.

No process within the rhizosphere is independent of a multitude of interacting components. Biophysical interactions within soils control, to some extent, all soil processes at all relevant scales. The pore channels act to guide the transport of substances and biota through the soil, and water films act essentially as valves, either reducing the flow of gas in the soil or aiding the movement of micro-organisms. Soil micro-organisms and carbon substrates act to stabilize the structural framework and affect the development of heterogeneity in soil structure within the profile. With the growing interest in soil–plant–microbe interactions, it is crucial to maintain a focus on the physical habitat in which these interactions occur and not to isolate each process within separate disciplines.

Soil structural heterogeneity is an underpinning framework for root–soil research. Increasingly, there is an urgent need for a more functional research base in soil–plant–microbial science. Incorporation of elements of structural parameters into research on soil microbiology and plant physiology will serve to

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increase the applicability of that research to real field and environmental problems.

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REFERENCES

Anderson, A. R. A., Young, I. M., Sleeman, B. D. & Griffiths, B. S. (1997). Nematode movement along a chemical gradient in a structurally heterogeneous environment. II. Theory. *Fundamental and Applied Nematology* **20**, 165–172.

Baker, J. M. & van Bavel, C. H. M. (1986). Resistance of plant roots to water loss. *Agronomy Journal* **78**, 641–644.

Bazin, M. J. & Prosser, J. I. (1992). Modelling microbial ecosystems. *Journal of Applied Bacteriology Symposium Supplement* **73**, 89s–95s.

Bengough, A. G. & Mullins, C. E. (1990). Mechanical impedance to root growth: a review of experimental techniques and root growth responses. *Journal of Soil Science* **41**, 341–358.

Blanchart, E., Bruand, A. & Lavelle, P. (1993). The physical structure of casts of *Millsonia anomala* (Oligochaeta: Megascolecidae) in shrub savannah soils (Côte d'Ivoire). *Geoderma* **56**, 119–132.

Bormann, F. H. (1957). Moisture transfer between plants through intertwined root systems. *Plant Physiology* **32**, 48–55.

Braunack, M. V. A. & Freebairn, D. M. (1988). The effect of bulk density on root growth. In *Proceedings of the 11th International Conference of the International Soil Tillage Research Organisation*, *Volume I*, pp. 25–30. Edinburgh, Scotland: ISTRO.

Bruand, A., Cousin, I., Nicoullaud, B., Duval, O. & Bégon, J. C. (1996). Backscattered electron scanning images of soil porosity for analyzing soil compaction around roots. *Soil Science Society of America Journal* **60**, 895–901.

Caldwell, M. M. & Manwaring, J. H. (1994). Hydraulic lift and soil nutrient heterogeneity. *Israel Journal of Plant Sciences* **42**, 321–330.

Chenu, C. (1993). Clay– or sand–polysaccharide associations as models for the interface between micro-organisms and soil–water related properties and micro-structure. *Geoderma* **56**, 143–156.

Cockroft, B., Barley, K. P. & Greacen, E. L. (1969). The penetration of clays by fine probes and root tips. *Australian Journal of Soil Research* **7**, 333–348.

Darrah, P. R. (1991). Models of the rhizosphere. I. Microbial population dynamics around a root releasing soluble and insoluble carbon. *Plant and Soil* **133**, 187–199.

Dawson, T. E. (1993). Hydraulic lift and water-use by plants – implications for water-balance, performance and plant–plant interactions. *Oecologia* **95**, 565–574.

Dexter, A. R. (1987). Compression of soil around roots. *Plant and Soil* **97**, 401–406.

Edgerton, D. L., Harris, J. A., Birch, P. & Bullock, P. (1995). Linear relationship between aggregate stability and microbial biomass in three restored soils. *Soil Biology and Biochemistry* **27**, 1499–1501.

Ferriss, R. S. (1981). Calculating rhizosphere size. *Phytopathology* **71**, 1229–1231.

Focht, D. D. (1992). Diffusional constraints on microbial processes in soil. *Soil Science* **154**, 300–307.

Foster, R. C. (1988). Microenvironments of soil microorganisms. *Biology and Fertility of Soils* **6**, 189–203.

Gilligan, C. A. (1979). Modelling rhizosphere infection. *Phytopathology* **69**, 782–784.

Gilligan, C. A. (1985). Probability models for host infection by soilborne fungi. *Phytopathology* **75**, 61–67.

Gilligan, C. A. & Bailey, D. J. (1997). Components of pathozone behaviour. *New Phytologist* **135**, 475–490.

Greacen, E. L., Farrell, D. A. & Cockroft, B. (1968). Soil resistance to metal probes and plant roots. In *Transactions of the 9th International Congress of Soil Science*, *Adelaide*, *Vol. 1* (Ed. J. W. Holmes), pp. 769–779. Sydney: International Society of Soil Science.

Grose, M. J., Gilligan, C. A., Spencer, D. & Goddard, B. V. D. (1996). Spatial heterogeneity of soil water around single roots: use of CT-scanning to predict fungal growth in the rhizosphere. *New Phytologist* **133**, 261–272.

Guidi, G., Poggio, G. & Petruzzelli, G. (1985). The porosity of soil aggregates from bulk soil and from soil adhering to roots. *Plant and Soil* **87**, 311–314.

Hall, D. G. M., Reeve, M. J., Thomasson, A. J. & Wright, V. F. (1977). *Water Retention, Porosity and Density of Field Soils. Soil Survey Technical Monograph No. 9*. Harpenden, Herts: Rothamsted Experimental Station.

Hawes, M. C. & Pueppke, S. G. (1986). Sloughed peripheral root cap cells: yield from different species and callus formation from single cells. *American Journal of Botany* **73**, 1466–1473.

Hettiaratchi, D. R. P. (1990). Soil compaction and root growth. *Philosophical Transactions of the Royal Society*, *London B* **329**, 343–355.

Jenny, H. & Grossenbacher, K. (1963). Root–soil boundary zones as seen in the electron microscope. *Soil Science Society of America Proceedings* **27**, 273–277.

Liddell, C. M. (1992). Experimental approach to measure the compression of soil around emerging coleoptiles. *Soil Biology and Biochemistry* **24**, 471–477.

MacFall, J. S., Johnson, G. A. & Kramer, P. J. (1991). Comparative water uptake by roots of different ages in seedlings of loblolly pine (*Pinus taeda* L.) *New Phytologist* **119**, 551–560.

McCully, M. E. (1995). Water efflux from the surface of field-grown grass roots. Observations by cryo-scanning electron microscopy. *Physiologia Plantarum* **95**, 217–224.

McCully, M. E. & Boyer, J. S. (1997). The expansion of maize root-cap mucilage during hydration. 3. Changes in water potential and water content. *Physiologia Plantarum* **99**, 169–177.

McCully, M. E. & Canny, M. J. (1989). Pathways and processes of water and nutrient movement in roots. In *Structural and Functional Aspects of Transport in Roots* (Eds B. C. Loughman *et al.*), pp. 3–14. New York: Kluwer Academic Publishers.

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Misra, R. K., Dexter, A. R. & Alston, A. M. (1986). Maximum axial and radial growth pressures of plant roots. *Plant and Soil* **95**, 315–326.

Molz, F. J. & Peterson, C. M. (1976). Water transport from roots to soil. *Agronomy Journal* **68**, 901–904.

Monteith, J. L. (1986). How do crops manipulate supply and demand? *Philosophical Transactions of the Royal Society of London A* **316**, 245–259.

Morel, J. L., Habib, L., Plantureux, S. & Guckert, A. (1991). Influence of maize root mucilage on soil aggregate stability. *Plant and Soil* **136**, 111–119.

Nye, P. H. & Tinker, P. B. (1977). *Solute Movement in the Soil–Root System*. *Studies in Ecology*, *Volume 4*. London: Blackwell Scientific Publications.

Odum, E. P. (1969). The strategy of ecosystem development. *Science* **164**, 262–270.

Parke, J. L., Moen, R., Rovira, A. D. & Bowen, G. D. (1986). Soil water flow affects the rhizosphere distribution of a seed-borne biological control agent, *Pseudomonas fluorescens*. *Soil Biology and Biochemistry* **18**, 583–588.

Passioura, J. B. (1988). Water transport in and to roots. *Annual Review of Plant Physiology and Plant Molecular Biology* **39**, 245–265.

Reid, J. B. & Goss, M. J. (1981). Effect of living roots of different plant species on the aggregate stability of two arable soils. *Journal of Soil Science* **32**, 521–541.

Reid, J. B., Goss, M. J. & Robertson, P. D. (1982). Relationship between the decreases in soil stability effected by the growth of maize roots and changes in organically bound iron and aluminium. *Journal of Soil Science* **33**, 397–410.

Richards, J. H. & Caldwell, M. M. (1987). Hydraulic lift, substantial water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**, 486–489.

Roberson, E. B., Sarig, S. & Firestone, M. K. (1991). Cover crop management of polysaccharide-mediated aggregation in an orchard soil. *Soil Science Society of America Journal* **55**, 734–739.

Roberson, E. B., Sarig, S., Shennan, C. & Firestone, M. K. (1995). Nutritional management of microbial polysaccharide production and aggregation in an agricultural soil. *Soil Science Society of America Journal* **59**, 1587–1594.

Rougier, M. & Chaboud, A. (1985). Mucilages secreted by roots and their biological function. *Israel Journal of Botany* **34**, 129–146.

Tisdall, J. M., Cockroft, B. & Uren, N. C. (1978). The stability of soil aggregates as affected by organic materials, microbial activity and physical disruption. *Australian Journal of Soil Research* **16**, 9–17.

Uren, N. C. & Reisenauer, H. M. (1988). The role of root exudates in nutrient acquisition. *Advances in Plant Nutrition* **3**, 79–114.

van Noordwijk, M., Kooistra, M. J., Boone, F. R., Veen, B. W. & Schoonderbeek, D. (1992). Root–soil contact of maize, as measured by a thin-section technique. I. Validity of the method. *Plant and Soil* **139**, 109–118.

Vetterlein, D. & Marschner, H. (1993). Use of a microtensiometer to study hydraulic lift in a sandy soil planted with pearl millet (*Pennisetum americanum* [L.] Leeke). *Plant and Soil* **149**, 275–282.

Waisel, Y., Eshel, A. & Kafkafi, U. (Eds) (1996). *Plant Roots: the Hidden Half*. New York: Marcel Dekker.

Wang, X.-L., Canny, M. J. & McCully, M. E. (1991). The water status of the roots of soil-grown maize in relation to the maturity of their xylem. *Physiologia Plantarum* **82**, 157–162.

Watt, M., McCully, M. E. & Canny, M. J. (1994). Formation and stabilization of rhizosheaths of *Zea mays* L. *Plant Physiology* **106**, 179–186.

Young, I. M. (1995). Variation in moisture contents between bulk soil and the rhizosheath of wheat (*Triticum aestivum* L. cv. Wembley). *New Phytologist* **130**, 135–139.

Young, I. M. & Mullins, C. E. (1991). Factors affecting the strength of undisturbed cores from soils with low structural stability. *Journal of Soil Science* **42**, 205–217.

Young, I. M., Mullins, C. E., Costigan, P. A. & Bengough, A. G. (1991). Hardsetting and structural regeneration in two unstable British sandy loams and their influence on crop growth. *Soil and Tillage Research* **19**, 383–394.

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