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ROOT FUNCTIONAL ARCHITECTURE: A FRAMEWORK FOR MODELLING THE INTERPLAY BETWEEN ROOTS AND SOIL

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ABSTRACT

Soil ecosystems support a plethora of intertwined biophysical and biochemical processes. Soil structure plays a central role in the formation and maintenance of soil biological activity by providing a diversified habitat for soil organisms and determining the movement and transport of the resources they rely upon. At the same time, the formation and preservation of soil structure and fertility is also strongly linked to soil biological activity through feedback loops. In most soil ecosystems, soil biological activity and associated processes are concentrated in the soil located around living plant roots and influenced by root activity, an environment known as the rhizosphere. Consequently, among the wide array of soil life forms, plants play a dominant role in the regulation of many soil processes. In this paper, we illustrate the functional complexity of soil ecosystems using specific examples of root-soil interactions and associated processes. Through examples taken from the literature, we examine the origins and variations in soil physical, chemical and biological properties and their impact on root growth. Next, we consider how the response of root systems to their environment affects resource acquisition by plants. Finally, we describe how the concept of root functional architecture can improve the integration of research advances from fields operating as independent disciplines and improve our understanding of soil ecosystems.

Keywords: root system / model / functional architecture / soil heterogeneity/ macropores/ review

INTRODUCTION

In the current context of food production intensification, agronomists must concentrate on finding new solutions to increase crop productivity while minimizing water and nutrient losses and soil degradation (Passioura, 2006). The design of sustainable cropping systems can only be achieved if sufficient knowledge about the biophysical context(s) in which they are intended to be implemented is available. A key to this challenge is to better understand the intricacies of soil biological, chemical and physical processes. In particular, improved knowledge about root-soil interactions could contribute to the design of practices that ensure optimized resource capture while providing leverage to minimize soil and water degradation, problems which increasingly plague most intensive cropping systems (Tilman et al. 2002).

Soil is a highly complex environment encompassing physical and chemical heterogeneity across a wide range of spatial and temporal scales. It bridges the mineral world with all the other trophic levels in the biosphere. Soil structure is central to such a fundamental linking role, as it provides the habitat for organisms and the pathway for essential resources they depend upon. In turn, soil biological activity impacts on the formation and preservation of soil structure and fertility. Although the array of soil life forms is quite extensive, e.g. bacteria, protozoa, fungi, nematodes, or macro-invertebrates, plants play a dominant role in the formation and maintenance of all other soil processes through root growth and functioning. Importantly, plants represent a major input of C to the soil: up to about a third of photosynthates allocated to roots can be lost to the soil as cap cells, mucilages, soluble exudates and lysates, and decaying tissues (Hawes et al., 2003; Hutsch et al., 2002; Nguyen 2003). Because of roots' inherent nutritional value as a carbon substrate and the wide range of metabolites that they secrete into the soil (Rovira 1965), rhizosphere soil and root surfaces are also the main habitats for many soil organisms. Many aspects related to soil heterogeneity, rhizosphere processes and root-soil interactions have been covered in three recent reviews (Doussan et al. 2003; Hinsinger et al 2005; Gregory 2006). As clearly outlined in these reviews, the heterogeneity of soil physical processes and their variation in space

and time are topics which have received much less attention than their biological and chemical counterparts.

In the first part of this manuscript, we review the main biological factors which influence soil physical and chemical heterogeneity from the micropore to the macropore scale. We show that it is somewhat artificial to separate soil physical processes from their chemical and biological analogues as they are almost systematically associated and in interaction with them. Due to their indisputable importance regarding soil functioning, roots represent a natural entry point for the study of the functional complexity of soil ecosystems. A second part of the paper focuses on root functional heterogeneity to examine how roots explore the soil and adapt to the soils' inherent physico-chemical heterogeneity. It is widely accepted that all roots have similar, if not identical functional characteristics (Zobel, 2003). However, recent work by Zobel et. al (2006) showed that even within roots <1mm in diameter, several functional classes can be identified based on their responses to environmental conditions. The concept of root functional architecture proposed by Zobel (2003) acknowledges this inherent complexity so that description of roots and root systems integrate the multiple genetically and anatomically determined functional root classes. In a third section, we examine how a modelling approach based on the concepts of functional architecture (Dunbabin 2002a,b; Doussan et al. 2006), has the potential to provide sharper insights into processes of soil exploration/utilization by roots. We also describe how these new developments in modelling open perspectives to i) quantify soil exploration by roots and root functioning at scales ranging from the individual root to the entire root system, and ii) study interacting soil physical, chemical and biological processes.

THE COMPLEX INTERPLAY BETWEEN SOIL PHYSICAL, CHEMICAL AND BIOLOGICAL PROCESSES FROM THE MICROPORE, TO THE MACROPORE SCALE

Physical and chemical heterogeneity is a common feature of most soils. Depending on soil

mineralogy, the formation of zones of highly heterogeneous soil strength can result from purely physical processes such as cracking/swelling or freezing-thawing cycles. Human activity such as agricultural practices induce structural modifications which, although generally limited to the first 10-30 cm of the soil profile, are more rapid than natural processes and thus tend to have 'traumatic' effects on soils (Whalley et al, 1995): e.g. subsoil compaction due to tillage, wheel traffic or trampling by cattle, formation of plough pans, slotting and deep ripping. Physico-chemical heterogeneity also occurs as local soil properties are progressively modified by pedogenesis (weathering and accumulation processes resulting in more or less differentiated soil horizons). Finally, an important part of soil physico-chemical heterogeneity results from biological activity such as perforation, ingestion, deposition. In the following paragraphs, we discuss some of the main biological factors influencing the formation of soil heterogeneity, from the micropore to the macropore scale.

Biological activity and soil heterogeneity at the micro- and meso-scales

Soil biota range in size from microscopic, e.g. bacteria or endomycorrhizal hyphae, to centimetric, e.g. earthworms or ants. Hence, soil biological activity impacts on soil heterogeneity at all scales ranging from the basic arrangement of soil elementary particles – textural scale, to the macroscopic arrangement of aggregates, macropores and soil layers – structural scale. Endomycorrhizal (or arbuscular mycorrhizal) hyphae are only about 12–15 μ m in diameter (Staddon et al. 2003) and so do not significantly modify the physical arrangement of soil particles. However, examination of field samples by scanning electron microscopy revealed that, due to their filamentous nature, fungal hyphae tend to tightly enmesh soil particles (Gupta and Germida 1988). In addition, as they are covered with polysaccharide rich mucilage, fungal hyphae can temporarily join together soil microaggregates, thus fostering the formation of stable macroaggregates (>0.25 mm) (Tisdall and Oades, 1982; Tisdall, 1991).

Although difficult to quantify accurately, indices of spatial correlation between bacterial densities, nutrient hotspots and different pore size classes have been reported by a number of authors (e.g. Gaillard et al. 1999; Nunan et al. 2003). Laboratory experiments conducted under controlled moisture conditions (Dorioz et al., 1993) showed that the microstructure of clay pastes is prone to modification by bacteria which induce polysaccharide-mediated aggregation of clay particles. In a series of experiments aimed at understanding the influence of soil matrix geometry on nitrogen mineralization and nitrification, Strong et al. (1998, 1999) investigated the relationships between pore size class, microbial activity and physico-chemical properties of an Australian red earth. They found that organic-N was concentrated in micropores $< 0.6 \mu\text{m}$ and in mesopores larger than $10\text{-}30 \mu\text{m}$ but not in the intermediate pore size class. They interpreted this finding as the result of, on the one hand, protection from microbial decomposition in micropores, and on the other hand, the fact that moisture conditions are less frequently favourable to microbial activity in the bigger mesopores than in the medium-sized ones (hence the scarcer amounts of organic-N in the latter than in the former). According to the scenario proposed by Strong et al. (1998), as microbial colonies consume organic substrates from within smaller mesopores and excrete extra cellular polysaccharides (EPS), mineral particles are rearranged, leading to increased mesoporosity at the expense of micro-porosity. The role of microbial activity in the formation of mesoporosity has been further confirmed by electron microscopy observations of field samples: increases in microbial colony size by cell multiplication or by EPS secretion were reported to be consistently associated with the re-arrangement of nearby clay minerals, to form compacted layers of overlapping clay platelets impregnated with EPS (Foster and Rovira 1978; Foster et al. 1983; Foster 1988; Chenu 1993). With time, such microbially generated mesopores can be reclaimed as micropores: EPS bound clay domains can be broken down by drying-wetting cycles, leading to the release of previously adsorbed organic compounds in the soil solution (Lund and Goksoyr 1980). Finally, Strong et al (1999) could link the micropore/mesopore balance with local redox processes related to microbial activity. They suggested that, under the anaerobic conditions which prevail in moist, micro-porous

soil volumes, the reduction of metallic oxides (typically Mn or Fe oxides) is enhanced and relieves the pH stress that N mineralising and nitrifying organisms would otherwise experience (as a result of H⁺ release following oxidation of C substrates). This example clearly highlights how interacting physical, chemical, and biological components of the soil induce the formation of microbial microsites and diffusion gradients which are important determinants for many soil functions.

Biological activity and soil heterogeneity at the macro-scale

Mesofauna and macrofauna are present at a coarser scale. Mesofauna are mainly microarthropods (100 µm to 2 mm) such as mites (acari) and collembola which do not have any known impact on soil particle arrangement. They are confined to pre-existing voids in the litter or soil and have negligible effects on soil heterogeneity (Lee and Foster, 1991). In contrast, soil macrofauna have major interactions with the soil. A few groups of larger soil invertebrates that are widely distributed and generally present in large numbers, namely earthworms, termites and ants (Lee and Foster, 1991) have the most significant effects on soil structure (provided that soil moisture is sufficient for these invertebrates to be active). Soil macrofauna have body sizes large enough to disrupt the physical make-up of most soils; for example, by burrowing, earthworms affect the transfer of water, air and nutrients through the soil (Edwards et al. 1989; Bouma 1991; McCoy et al. 1994; Li and Ghodrati 1995). In general, the effect of termite and ant activity on soil structure is less extensive than that resulting from earthworm activity: nest walls are consolidated by sticking together soil particles with excreta or salivary secretions, frequently forming massive cemented layers which locally reduce water infiltration (Lee and Foster, 1991). The physical disruption induced by earthworm burrowing is accompanied by many biochemical modifications (Brown, 1995; Parkin and Berry, 1999; Tiunov and Scheu, 1999). For example, earthworms have a significant impact on the incorporation and distribution of organic matter in the soil (Shuster et al. 2001). They selectively activate mineralization and humification processes, hence

promoting short and rapid cycling of nutrients and assimilable carbohydrates (Lavelle, 1988); it was reported that in some soils, 40% of all aerobic N₂-fixing bacteria, 13% of anaerobic N₂ fixers and 16% of denitrifying bacteria were located in a thin layer lining earthworm burrows (Bhatnagar 1975 cited in Anderson 1988). As a result of their feeding activities, they produce casts which have higher CEC, soluble carbohydrates, organic and mineral N, phosphatase and urease activity and available P than soils from which they are derived (Satchell, 1983). Schrader et al (1995) also indicated that there is a positive correlation between the organic C content of worm casts and their tensile strength, and that worm casts have a higher structural stability than artificially constructed aggregates. Thus, as a consequence of the many local modifications they induce, earthworms play a central role in soil ecosystems and influence both directly and indirectly root distribution and growth (Volkmar 1996; Lavelle 1997).

Plant roots and soil heterogeneity

Roots obviously alter soil physico-chemical properties at the macroscopic scale in many ways. Growing root apices induce a re-orientation of the soil particles and secrete extra cellular polysaccharides (EPS) which locally bind soil particles (Cheshire 1979; Tisdall et Oades, 1982; Dorioz et al., 1993). These two processes result in a general packing effect and the formation of macropores (Bruand et al. 1992, 1996; Jaillard and Callot, 1987). Field observations have confirmed that some deep-rooted perennial plant species can significantly alter soil macroporosity (e.g. Cresswell and Kirkegaard, 1995; Stirzaker et al. 1996; Lesturgez et al. 2004). Root water uptake induces gradients in soil water content, which, depending on soil texture and mineralogy, can lead to cracking (Lafolie et al. 1991; Bruckler et al. 1991), and also contribute to soil aggregation (Tri and Monnier, 1973). In association with the local re-arrangement of soil particles that growing roots create in their immediate vicinity, there is also the development of a chemically and microbiologically differentiated environment, generally known as the rhizosphere (Darrah 1993; Hinsinger, 1998). In some plants species, in particular graminates, this root-affected soil can take the form of

rhizosheaths which are physically bound to parts of the root system (McCully, 1995; Watt et al., 1994).

ROOT HETEROGENEITY, ROOT GROWTH AND RESOURCE CAPTURE BY ROOTS

As recently outlined by Hutchings and John (2004), most studies on root growth are conducted following the premise that soil conditions are homogeneous, leaving serious gaps in our understanding of plant functioning under natural and managed conditions and of how they take advantage of patchy soil conditions. As illustrated by the examples discussed in the previous sections of this paper, soils are heterogeneous environments constantly reorganised by soil organisms and growing plants, at all scales from the micropore to the macropore. In the following sections we discuss our current understanding of the mechanisms used by roots to grow and assimilate resources in such a heterogeneous environment.

Variations in root properties among root types and along individual roots

Roots can be classified into several categories according to their ontogenesis and functions. Detail about nomenclatures used to describe root types and root system architectures can be found in Harper et al. (1991), Klepper (1992) Pagès et al., (1989; 2000) and Zobel (2005a,b). Many reports clearly indicate that different root types play different functional roles. For example, in wheat, leaf expansion is more severely reduced when drought affects seminal rather than nodal roots (Volkmar, 1997). Similarly, the contribution (in terms of resource acquisition) of the seminal root system to the whole plant exceeds what could be expected from its fractional mass (Waisel and Eshel, 2002). Navara (1987) showed that the radicle and seminal roots of maize play a dominant role in supplying water during a significant part of the plant life span, while the nodal root system seems to be more heavily involved in the uptake of resources such as phosphate (Mistrik and Mistrikova, 1995). In barley root systems,

although nitrate uptake rates decrease overall between the vegetative and reproductive stages, they tend to remain constant in the nodal root system (Mattson et al., 1993). Lazof et al. (1992) showed that nitrate uptake rates (per unit dry weight) of the primary axis of young maize plants was up to 68% of that of the lateral roots. Waisel and Eshel (1992) demonstrated variations in Cl and K uptake between taproot and laterals in pea. Mature lateral roots of maize lowered the pH at the soil-root interface while the parent root made it more alkaline (Marschner, 1990).

Important changes in physiological properties also occur along individual roots. Some of these changes are related to root ontogenesis i.e. as root tissues get older, mature and differentiate, their physiological status evolves: as a consequence, different uptake rates and root functions are observed, at increasing distances from the root tip (Clarkson, 1996). For example, high variations in root respiration were found along primary roots of *Prunus persica* (Bidel et al., 2000), not only in the vicinity of the apex but up to about 20 cm from root tips. Depending on nitrogen availability, parts of some roots can release protons and participate in the acidification of the immediate root environment, while others release hydroxyl ions (Jaillard et al., 2000). Nitrate and ammonium uptake were observed to vary along roots, with zones of active (generally in the apical region) and passive uptake (Cruz et al., 1995; Lazof et al., 1992). Variations in the uptake and translocation of other ions (P,K,Ca...) along roots were also reported (Clarkson, 1996). In the field, cortical senescence in older root parts seems relatively common in cereals and other grasses (Robinson, 1991). Cortical senescence may weaken ion uptake because of physiological decay but also through disruption of soil-to-root transport pathway.

Root system development and architecture *in situ*

Studies throughout the 20th century established that the overall architecture of root systems *in situ* (e.g. dominance of the main axis, branching pattern...) is generally more complex and subject to great inter- and intra-specific variability (Cannon, 1949; Kutschera, 1960; Weaver, 1919) than that of roots grown under standard lab conditions (e.g. in agar). The respective

importance of the primary and adventitious root systems, i.e. the relative growth rates of main axes and laterals or the number of branching orders, varies across plant species. Different families of plant species which make up the vegetation in a given ecosystem are genetically programmed to occupy different niches, and thus often use different soil exploration strategies. Two different soil exploration strategies, reflected by different root system architectures are illustrated in Figure 1, which shows the typical rooting patterns of a perennial monocotyledon (*Lolium multiflorum*) and a perennial dicotyledon species (*Achillea millefolium*) (Kutschera 1960). *Lolium multiflorum* (Figure 1A) develops a centralized adventice root system, often referred to as fasciculated system. Such a root system, in which main roots are continuously emitted from the plant base according to a species specific emission rate, is typical of grasses and other monocotyledons. On the other hand, *Achillea millefolium* (Figure 1B) grows a non-centralized adventice root system, in which a network of rhizomes simultaneously emits branches and main roots. Such genetically controlled growth patterns are often modulated depending on the environmental conditions experienced by plants, leading Harper et al. (1991), to define the development and functioning of a given root system as an evolutionary response to the spatio-temporal variability of resource availability and the corresponding constraints to growth. Possible effects of such responses on root system architecture are illustrated in Figure 2. Variable soil conditions experienced locally by plant roots trigger, within species-specific limits, a range of physiological responses which help the plant minimise the potential stress arising from soil heterogeneity and enable it to take advantage of “better-than-average” conditions (Drew, 1975; Robinson et al. 1999). Such plastic root responses to heterogeneous supplies of nutrients have been extensively reviewed by Hodge (2004, 2006); Plants have developed a range of complex strategies to exploit the soil's inherent patchiness, such as proliferation, segregation, aggregative root placement (Bartelheimer et al., 2006) or pre-emption of nutrient supply (Craine et al., 2005). Hence, root system development/expansion can be conceptualized as the allocation of assimilates to a population of individual root apices capable of independent, though coordinated, morphological and physiological responses to their immediate environment.

Thus, to a large extent, the overall functioning of a root system actually corresponds to independent physiological activities coordinated at the whole root system level and varying axially along single roots in relation to their age.

The presence of zones of high mechanical resistance is one of the most common physical limitations to soil exploration by roots (Hoad et al., 1992). In cultivated soils, the location, lateral extension and thickness of zones of high resistance to penetration vary during the growing season (Castrignano et al., 2002). In soil volumes of higher strength the development of soil structure is of paramount importance to root penetration (Tardieu and Manichon, 1986; Tardieu and Katerji, 1991; Figure 3A): increases in soil strength reduce root elongation, alter root diameters and the average number of laterals on primary axes (Bennie, 1996; Dexter 1987; Figure 3B). In soils which impede root growth (e.g. because of high resistance to penetration) successive generations of roots tend to reuse paths of least mechanical resistance such as pre-existing structural features like cracks, biopores or soil casts excreted by soil macrofauna (Rasse and Smucker, 1998). This co-location of roots and macropores (McKenzie et al., 1995; Volkmar, 1996; Stewart et al, 1999) leads to the formation of a specific environment which differs significantly chemically and biologically from the bulk soil (Pierret et al., 1999; Pankhurst et al., 2002).

Soil exploration versus resource acquisition

Because, as described above, root systems are not uniformly and constantly active, soil exploration by plant roots is not a reliable indicator of soil resource exploitation. It has been clearly demonstrated that, if homogeneous root behaviour is assumed to model water and nitrate uptake rates, predicted values at the entire root system level are substantially over-estimated: based on such an exercise, Robinson (1991) inferred that, on average, only 10% and 30% of the total root length of a given root system is effectively involved in nitrate and water uptake respectively. Thus, to understand resource acquisition by plant roots, it is essential to determine (i) which fraction of the root system is active (e.g. which root order(s) or which region(s) of the root system including several root orders), and (ii) how the spatial

distribution of root activity within the root system varies with time and/or depending on environmental conditions. From the point of view of resource acquisition, a root system, must be regarded as a population of individual roots behaving (i) differently and independently from each other (Waisel and Eshel, 1992) (although coordinated to some degree at the root system level), (ii) as a function of tissue differentiation and (iii) in response to changing environmental conditions (plasticity).

Root system plasticity and uptake optimisation

. Roots probably evolved plastic responses to their environment as they differentiated as specialised tissues throughout geological times (Raven and Edwards, 2001), optimised to explore and utilise resources in heterogeneous soils (Leyser and Fitter, 1998). Root plasticity is also a response to intra- and inter-specific competition. For example, Robinson (2001) showed that plastic root responses are triggered by intra-specific competition in a wheat monoculture but do not necessarily lead to greater uptake rates. Nutrient availability is known to influence many facets of root system morphology (Ford and Lorenzo, 2001): root branching, root growth (with growth of main axes generally less affected by nutritional effects than higher order axes), root diameter, root angle (for example, low P availability decreases the angle of emission of basal roots in bean, soybean and pea (Liao et al., 2001)), root hair length and density, as well as production of specific root types (cluster roots (Skene, 2000) or drought-induced roots (Vartanian, 1996)). The response of plants to variations in the location of nutrients has been well studied (see review by Robinson, 1994) compared to the influence of temporal variations in nutrient concentrations on root plasticity. Experimental observations of root responses to variations in the spatio-temporal availability of nutrients have generally been made under conditions where access to nutrients was artificially reduced; For example, a classic experimental design consists of providing nutrients to a small portion of the root system only, while the rest of it grows in nutrient poor or sterile soil (Drew and Saker, 1975). Roots respond to such a heterogeneous system in two ways

(Robinson, 1996): (i) the nutrient inflow rate increases but then returns to normal within hours, (ii) roots proliferate towards and within the nutrient rich patch over a period of several days, while root growth in the rest of the root system is inhibited. These trends vary depending on the plant species, with the induced increases in root growth and nutrient uptake varying over one order of magnitude or with a total lack of response in some species (Robinson, 1996). The stimulation in uptake rate seems to be sensitive to the nutrient considered and the duration of the starvation period. Root proliferation appears less dependent on the nutrient considered (except for K in some species). Localised responses are generally assumed to be caused by direct nutritional benefits to the roots directly exposed to nutrient patches, but there is some evidence that they can also involve indirect, sophisticated mechanisms: for example Zhang et al. (1999) proposed a dual pathway for NO_3^- in *Arabidopsis thaliana* in which the NO_3^- ion is acting as a signal, rather than a nutrient, and root branching is modulated by opposing signals from the plant's internal N status and the external supply of NO_3^- .

MODELLING ROOT FUNCTIONING AND SOIL EXPLORATION BY ROOTS

In most crop models, water and nutrient uptake are predicted on the basis of synthetic descriptors such as the root density (e.g. length, biomass or surface area... per unit soil volume). Such descriptors are indicative of soil exploration by roots if it can be assumed that roots are regularly distributed in the soil. However, under field conditions, the assumption of a regular distribution of roots does not hold (Tardieu, 1988) and root distribution within the soil has a strong influence on resource acquisition by plants (Lynch and Nielsen, 1996; Pagès, 2002; Pagès et al., 2000). Consequently, summary parameters such as root density are not sufficient to investigate the detailed development and functioning of root systems: it is necessary to include details about root architecture and growth dynamics in models to gain sharper insights into soil exploration/utilization processes. As they include explicit quantitative information about the soil volume that a given root system accesses and influences, as well as about the location and number of roots, models of root system

architecture provide a unique opportunity to understand soil exploration by roots. Conceptually, models of root system architecture consist of 3-dimensional sets of connected axes or segments, each characterised by properties such as, e.g., diameter, water or nutrient uptake ability. Existing models of root system architecture include variable degrees of dynamic complexity which have been extensively reviewed by Doussan et al. (2003). Explicit models of root system architecture are also valuable tools for including affects of heterogeneous soil conditions on root growth, at the scale of the individual root segment through to the whole root system.

Using root architecture models to assess the interactions between roots and their chemical environment

Using root architectural modelling, Ge et al. (2000) studied the effect of altered gravitropism of the basal roots of bean plants (the position of which varied from shallow to deep) in order to study their importance in P acquisition efficiency. The authors considered both a homogeneous P distribution and a stratified distribution with high P concentrations in the top 10 cm of the soil profile. In both cases, shallower root systems explored more soil (per unit root biomass) than deeper systems because of reduced inter-root competition (i.e. the overlap of depletion zones corresponding to neighbour roots was reduced in shallow root systems- Figure 4 A and 4 B).

Somma et al. (1998) and Dunbabin et al. (2002a) also incorporated aspects of the effects of nutrient availability on root system development in their root architectural models. In Somma et al's model (1998) the effect of nitrate on root growth was implemented via a linear impedance function which mimics the fact that root growth remains unaffected by nutrient concentrations as long as they fall within ranges which are both plant species- and nutrient-specific. For each growth step, an actual elongation rate is computed for each individual root apex, based on an unimpeded elongation (function of available photosynthetic assimilates) scaled according to temperature, soil strength and soil nutrient concentration impedance

factors. Figure 5 shows an example output from this model: the simulated root system of a 25 day old barley plant grown with water and NO_3^- supplied through drippers located on the soil surface. NO_3^- was either applied continuously (Figure 5A), or for a finite time at the beginning of the simulation (Figure 5B). The total amount of applied N was the same in the two cases. In the first case, simulations showed that N concentrations remain higher in the upper part of the soil and root density decreases with depth. In the second case, the NO_3^- plume moved downwards following the application and caused a greater root density in the central part of the soil. Interestingly, peaks in root length density and NO_3^- concentration did not coincide; a feature linked to the relative rates of root growth and the downwards percolation of NO_3^- .

More recently, Dunbabin et al. (2002a) encapsulated a more subtle description of root system plasticity into the root architecture ROOTMAP, initially developed by Art Diggle in Western Australia. This model's fundamental principle is to combine, at the whole plant scale, the demand for individual resources and, at the local scale, the ability of the various components of the root system to supply resources, thus driving the allocation of assimilates to the most rewarding parts of the growing root system. Depending on the soil conditions defined at the onset of numerical experiments (i.e. runs of the model aimed at testing scenarios consisting of different N and water supply patterns), the architecture and uptake efficiency of the root systems produced by the model resulted, at least in part, from the environmental conditions roots experienced throughout growth. Hence, this model simulates both a local 'sensing' response and a whole root system response: inflow and root proliferation plasticity are features which can be modelled with this approach. The authors tested their model's performance against laboratory and field experiments with Lupin, using nitrate as an example nutrient (Dunbabin et al., 2002a,b). Nitrate was supplied to the plants every second day, according to i) a static supply pattern (same random distribution of nutrient patches along the soil profile for every successive application) or ii) a dynamic supply (new random distribution of nutrient patches with every successive application). Figure 6 shows the results yielded by this model for two extreme root system topologies

(herringbone and dichotomous; from Dunbabin et al., 2001). In the case of static nitrate supply, due to root plasticity (both morphological and functional), the dichotomous system is more efficient than the herringbone one. In the case of dynamic N supply, the herringbone system appears to be more efficient than the dichotomous one, and the latter gains almost no efficiency in uptake from plasticity.

Using root architecture models to assess the interactions between roots and their physical environment

Several explicit models of root architecture incorporated the influence of soil temperature on root growth or root appearance, using a thermal time scale (Diggle, 1988; Pagès et al., 1989) or a reduction coefficient which reduces root growth rates (Clausnitzer and Hopmans, 1994). The effect of soil strength has also been included, by means, generally, of indirect variables such as soil bulk density or water content (Clausnitzer and Hopmans, 1994; Pagès, 1999; Figure 7A and 7B) combined with empirical functions which reduce optimal growth rates and alter root growth direction. To test the influence of hydrotropism on root growth in slopes, Tsutsumi et al. (2003) used an explicit model of root architecture that includes a sensing mechanism of water flux gradients near root tips to modulate root bending.

Currently, the modelling of the interactions between growing roots and their physical environment remains very basic. Prusinkiewicz (1998) presented a modified version of Diggle's ROOTMAP (Diggle 1988) which included root responses to mechanical obstacles (rocks) in the soil (Figure 7C). Recently, our research group initiated a new project aimed at testing the influence of soil structure on root growth and water uptake. Technically, this modelling exercise is based on coupling a simplified model of soil structure with a modified version of the model of root hydraulic architecture developed by Doussan et al. (1998a). The simplified model of soil structure consists of a 1.5 m cubic volume with a 5 cm seed-bed, a 25 cm thick tilled layer, a 3 cm plough layer and an ~1.2 m deep subsoil. Soil structure in the tilled layer is described as a distribution of dense clods embedded in a looser matrix. Clod

shape and size distributions were simulated on the basis of field observations made in northern France (Desbourdes-Coutadeur 2002). For the subsoil, a soil density gradient combined with a macropore network was used to represent soil structure. Objects considered as macropores were generated using the model developed by Capowiez and Bastardie (Bastardie et al., 2002) to describe earthworm burrowing behaviour. Burrows 2-3 and 5 mm in diameter respectively were simulated, corresponding to a mixed population of endogeic - *Aporrectodea caliginosa*- and anecic - *Lumbricus terrestris* - worms, with individual densities corresponding to field observations made in NE France. During the root growth simulation period, a local soil impedance factor was computed for each cell of the structured soil volume by combining the local soil bulk density with the local soil water content (deduced from an initial soil water profile which was altered at each time step so as to mimic soil drying). This local soil impedance factor was used to modulate root elongation depending on local soil moisture and bulk density conditions (from 1, unimpeded growth to 0, stalled apical growth). At this stage, extremely simplified rules have been used regarding root response to the presence of soil structural features: i) if a macropore is present within the voxel in which a given root tip is entering, following the elongation corresponding to a simulated time step, the root tip continues its growth inside the macropore if a randomly generated number is higher than an arbitrarily set threshold (otherwise, it is assumed that contact between root tip and macropore did not occur); ii) once inside a macropore, a root tip is forced to follow the whole extension of the macropore before it can grow back in the soil matrix; iii) root elongation remains totally unimpeded as long as the root tip remains “trapped” in the macropore. At present, rules regarding the alteration of branching patterns in response to local impedance to root growth have not yet been added to the model. Even though extremely simplified, this model opens new avenues for understanding the effect of soil structure and soil structure manipulation on root growth and functioning. At this stage, it is possible to generate maize root systems whose architecture is clearly altered by the presence of soil structural features (Fig 8). In the near future, we hope to use this model to assess the effect of different degrees of soil structural constraints to root growth on root

water uptake.

Encapsulating root functional heterogeneity into root models

The example of root water uptake perfectly illustrates how root functional heterogeneity can be taken into account using root architectural models. As relatively impermeable structures differentiate away from the root tip (suberization), root water uptake is increasingly impeded along the radial pathway (which concerns water transport from the soil to xylem vessels). Symmetrically, with the presence of increasingly opened xylem vessels away from the root tip, axial water transport to the stem is facilitated. In maize main axes, late metaxylem vessels (i.e. xylem of high water carrying capacity) are only fully open at distances up to 20-30 cm from the apex (Wenzel et al., 1989). Based on experimental measurements of the axial and radial hydraulic conductance of maize roots (Varney and Canny, 1993), Doussan et al. (1998a,b) were able to model the spatial variability of root hydraulic conductance within the root system of maize. They showed that this spatial variability led to the formation of a heterogeneous water uptake pattern, even when soil water is readily and evenly available to all roots (Figure 9). A different water uptake pattern was found for the perennial root system of *Prunus* (Doussan et al., 1999), indicating that genetic differences influence root water uptake heterogeneity.

Recently, Doussan et al. (2006) developed their root architectural model further so as to couple the effect of local soil and root hydraulic properties with the formation and evolution of root water uptake patterns, at the scale of the entire root system. This new model provides information about root system functional architecture and hydraulic continuity between plant and soil. Both experiments (using light and X-ray transmission imaging of root water uptake (Garrigues et al., 2006)) and modelling concurred to showing that as water is extracted from the growth medium by the plants (*Lupinus angustifolius*), a water uptake front forms and moves downward along the root system (as soil dries) (Figure 10). This uptake front's spatial extension and displacement along roots was closely related to local root and soil hydraulic

properties. In particular, the water retention properties of the growth medium strongly influenced the characteristics of the front: a sharp front formed in a dominantly sandy medium, whereas, in a sandy-clay loam, the front's shape was very attenuated. Comparisons between tap rooted and fibrous root system architectures grown in a sandy medium, showed that the tap rooted architecture induced a more spatially concentrated uptake zone (near the soil surface) with higher flux rates, but with a xylem water potential at the base of the root system twice as low as in the fibrous architecture. Modelling provided evidence that hydraulic lift can occur when transpiration declines at night, particularly in a growth medium prone to abrupt variations in soil water potential (sand). Overall, this new way of modelling soil-to-root water transfer, demonstrated that the concept of root functional architecture is valuable for studying water uptake in relation to both plant and soil heterogeneity. We envisage extensions of this approach to analyse root uptake, the distribution of root hydraulic conductance, or the influence of heterogeneous conditions (localised irrigation, root clumping), depending on genetically selected root architectural traits.

CONCLUSIONS

Models based on the concept of root functional architecture provide a unifying framework for integrating root and soil heterogeneity and their complex interaction. Such a modelling tool represents a unique opportunity to unify research advances from fields which operate as independent disciplines (e.g. results obtained using novel observation techniques such as non-destructive and cryo-scanning imaging of roots under field conditions (Pierret et al., 2003; McCully, 1999), micro-sensors (Portefield, 2002); root-pressure probes (Steudle, 2000)). It can be applied to the analysis of root water and nutrient uptake as a function of root architectural traits (genetically selected), distribution of root properties within the root system (hydraulic conductivity, nutrient uptake ability) or heterogeneous environmental conditions (e.g, localised water and/or nutrient availability). Models of root functional architecture could also prove useful for crop improvement as they can be used to derive robust bio-physical indexes characteristic of some crop/environmental combinations, such as improved root sink

terms for water uptake modelling. The many processes which can be investigated using the modelling of root functional architecture include:

- changes in root system morphology resulting from intra or inter-specific competition between plants (Collet et al., 2006), including allelopathy (Vaughan and Ord, 1991);
- interactions between roots and mycorrhizas or roots and microorganisms, which colonize parts of the soil volume and fine soil pores inaccessible to roots, and have been reported to alter root system architecture (Hooker et al., 1992);
- mobilisation of nutrients by roots via the release of mucilage, organic acids, complexing agents... (Hinsinger, 1998) and corresponding modifications of soil chemical properties in the vicinity of roots ;
- Occurrence and functioning of specialized roots: cluster roots, drought-induced roots, hairy roots...

To date, the majority of studies on roots have been conducted based on false premises of homogeneous soil conditions leaving serious gaps in our understanding of plant functioning under field conditions (Hutchings and John, 2004) and a lot remains to be understood about 'how real roots work' (McCully, 1995). In the current global context of food production intensification, further knowledge about the interplay between soil biochemical processes and soil mineral constituents, such as root-soil interactions, is urgently needed to increase crop productivity while minimizing water and nutrient losses and soil degradation. We believe that models of root functional architecture will play a key role in the design and testing of sustainable cropping systems.

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FIGURE CAPTIONS

Figure 1. Comparison between the rooting patterns of a perennial monocotyledon (*Lolium multiflorum* A) and a perennial dicotyledon species (*Achillea millefolium* B). (from Kutschera, 1960).

Figure 2. Effects of localised (i) nutrient supply and (ii) physical constraint on the root system architecture of a monocotyledon and a dicotyledon. Root system architecture of a Barley plants (*Hordeum vulgare* cv Proctor) uniformly supplied with nitrate (A), or supplied with nitrate through a banded treatment (B). The banded treatment triggered root proliferation in the zone of nitrate supply (Drew, 1975). Comparison of the architectures of two *Lupinus angustifolius* root systems: physically unconstrained growth conditions (C), and taproot growth stopped by a physical obstacle at an early developmental stage (D).

Figure 3. (A) Root impact map illustrating soil exploration by roots in compacted soil horizons in which cracks represent paths of least resistance preferentially explored by roots (Tardieu and Katerji, 1991). (B) A model for relative root elongation rate as a function of matric potential, at different levels of soil strength Q_p (Mpa), measured by a penetrometer (Dexter, 1987): as soil strength increases and soil is drier, relative root elongation (R/R_{max}) decreases.

Figure 4: Simulation of the influence of different degree of basal root gravitropism on the exploitation of P by bean root systems. The depletion zone of P is represented by diffusion of P to the root with time (Diffusion coefficient $10^{-8} \text{ cm}^2 \text{ s}^{-1}$). A) The bean root systems simulated with different rooting pattern (shallow; Carioca, an actual cultivar, and deep). B) Volume of the overlapping exploited zones for the three root system types. C) P uptake by the three simulated root systems at the end of simulation (320 h), in the case of a stratified soil profile of P (P concentration is higher in the first 20 cm of soil). (from Ge et al., 2000).

Figure 5: Simulated 3D root architecture (coupled with water and nitrate transfer and uptake by the root system) with corresponding root density and nitrate concentration distribution for (A) continuous supply of nitrogen by drippers and (B) the same amount of nitrogen, but supplied at the beginning of the simulation period (from Somma et al., 1998).

Figure 6. Simulation of nitrate uptake efficiency with an architecture model taking into account both inflow and morphological plasticity of the root system. Nitrate is distributed in the soil as small patches. The efficiency of uptake with plasticity is relative to the same root system with no plasticity response. Root systems are (A) herringbone system and (B) dichotomous system. In the dynamic supply case, the nutrient patches are randomly re-distributed in space, which is not the case for static supply (from Dunbabin et al., 2001).

Figure 7. Simulation of maize root system architecture interacting with the environment. A plough pan layer impedes root growth at 35 cm depth. (A) General morphology of the simulated maize plant. (B) Simulated (+) and observed (•) root profiles, obtained by counting the number of colonised cells (2 x 2 cm) on vertical grids. The horizontal bar represents one standard deviation. (from Pagès, 1999). (C) A simple example of simulated root growth around mechanical obstacles (rocks) in a homogeneous soil (from Prusinkiewicz, 1998).

Figure 8. Modelling of the interactions between roots and soil structure. (A) Comparison between two 100-day-old maize root systems, the first one (left hand side) grown in a homogeneous soil volume and the second (right hand side) grown in a structured soil consisting of a 25 cm thick tilled layer with distributed dense clods, a 3 cm plough layer and an ~1.2 m deep subsoil with biopores (earthworm burrows). In the case of the structured soil, the interactions between growing roots and soil structure have led to reduced rooting depth and lateral expansion of the root system. This is largely due to the trapping of roots in macropores at certain soil depths (50-55 cm in particular), as shown by the high occurrence

of root-to-macropore distances less than the voxel size (1 cm) (B).

Figure 9. Distribution of water uptake fluxes within a simulated maize root system. Water uptake is simulated by taking into account the variability of the root hydraulic conductance in the root system (from Doussan et al., 1999).

Figure 10. Simulation of the propagation of a water uptake front across the root system of a 50 day-old narrow leaf lupin with fibrous root system, growing in a sandy rhizotron. Length scale in cm. Distribution of calculated water uptake within the root system 1.5, 5, 7 9 and 11.5h after the beginning of an uptake experiment. The rates are expressed as flux density (i.e. volumetric flow rate normalized to the root surface area ($\text{cm}^3 \cdot \text{cm}^{-2} \cdot \text{s}^{-1}$)). The red lines show the downwardly moving zone of active water uptake. The green colour shows negative flux rates, i.e. water exsorption by roots (from Doussan et al., 2006).