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**The Proceedings of the International Plant Nutrition Colloquium
XVI**

Title

Rhizosphere processes : the roots of ecological intensification of agroecosystems

Permalink

<https://escholarship.org/uc/item/275198wg>

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Publication Date

2009-07-30

Peer reviewed

Introduction – The routes of ecological intensification of agroecosystems

Over the last 50 years, human beings have modified the ecosystems to an unprecedented point in humankind history, in order to meet the increasing world demand in food, drinking water, wood, fibers and energy (Tilman 1999). Such changes have contributed to considerably improving humankind well-being, but also to a degradation of numerous ecosystem services. Prediction models forecast further degradation of ecosystem services in the coming 50 years, if management strategies remain unchanged (Tilman et al. 2001 and 2002). The scientific challenge is considerable : how to feed the world and its increasing population in a context of limited changes of land use, i.e. a limited increase in productive arable land surface area (Vance et al. 2003). Current levels of agroecosystem productivity thus need to be further increased sustainably, i.e. both environmentally and economically, in order to preserve ecosystem services. There is thus a need for an ecological intensification of agroecosystems, in order to cover global food demand while decreasing agricultural inputs such as fertilisers (Cassman 1999).

The Millennium Ecosystem Assessment underlined that the cycles of nutrients, especially nitrogen (N) and phosphorus (P) were among the most affected ecosystem services, leading to a massive and fast-increasing eutrophication of aquatic ecosystems (Mackenzie et al. 2002), contamination of groundwaters by nitrate and emission of greenhouse gas (Vitousek et al. 1997). These are the consequence of the considerable increase in agricultural inputs and the steady decrease of their efficiency (Tilman et al. 2002) which occurred during the Green Revolution : from 1965 to 2000, the doubling of cereal production was accompanied by a 3.5- and 6.9-fold increase in the amounts of P and N fertilisers applied, respectively (Tilman 1999). Pursuing such an increase in N and P fertiliser application is no longer an option. For P, the fast exhaustion of high grade phosphate ores worldwide within about 90 years at the current rate of consumption of P fertilisers (Herring and Fantel 1993 ; Runge-Metzger 1995 ; Stewart et al. 2005) clearly challenges the sustainability of current P fertiliser use in developed countries (Cordell et al. 2009). Increasing the efficiency of nutrients to plants while decreasing nutrient inputs means that better exploration and exploitation of soil resources must be achieved in agroecosystems. For the purpose of this second Green Revolution, one needs to better know what are the intimate processes and factors that govern the acquisition of soil nutrients by plants, with solutions pertaining to plant roots (Lynch 2007). The aim of this review is to address this issue, with a particular focus on rhizosphere processes.

Rhizosphere biophysical processes

The acquisition of nutrients by plants requires the transfer of nutrients towards the root surface, prior to uptake, as accounted for by conventional models of plant nutrition (Barber 1995). Transfer processes playing a key role in that respect are mass-flow and diffusion, the relative contribution of which varies from a nutrient to another, and depends on plant requirements and nutrient availability in the soil, especially its concentration in the soil solution. This was first modelled by Nye and Mariott (1969) in the case of a single root model, assuming a Michaelis-Menten formalism for nutrient absorption across the root surface. In most nutrient uptake models deriving from those, the central hypothesis is that

the driving force of nutrient acquisition is the absorption process which results in a decrease of nutrient concentration at the surface of the root, leading to a diffusion gradient in the rhizosphere. Experimental evidence for nutrient depletion occurring in the rhizosphere is especially documented for poorly mobile major nutrients such as potassium (K) or P (Kuchenbuch and Jungk 1982 ; Hendricks et al. 1981 ; Jungk and Claassen 1986 ; Hinsinger 1998 and 2001; Jungk 2002). For such nutrients, mass-flow marginally contributes to the transfer towards the root surface as K and P usually occur at rather low concentrations in the soil solution. Mass-flow can however contribute a larger proportion of nitrate transfer towards the root surface, although depletion is expected to occur because of large N requirements of plants. There has been some reports of more complex patterns of nutrient distribution in the rhizosphere, such as a combination of depletion at the very root surface with nutrient accumulation occurring farther away from the root surface, relative to the bulk soil, as shown for P (Hübel and Beck 1993 ; Hinsinger and Gilkes 1996 ; Hinsinger 1998 and 2001; Hinsinger et al. 2008). Recent measurements conducted in our group after sampling the rhizosphere *in situ* in various field-grown plant species have further shown that depletion of P may be an exception rather than the rule in low input conditions. Such findings invalidate classical models of nutrient acquisition.

Further refinements of the Nye and Mariott (1969) derived models consisted to upscale from the root segment to the whole root system, which needed to account for root growth (Baldwin et al. 1973 ; Claassen and Barber 1976 ; De Willigen et al. 2002). When applied to nutrients such as K and P, such models have generally proved quite efficient at predicting the acquisition over time scales of days or weeks in the case of soils receiving high K or P inputs, but failed in low input conditions (Brewster et al. 1976 ; Schenk and Barber 1980 ; Lu and Miller 1994 ; Mollier et al. 2008). Under such conditions, those models systematically underestimate the actual uptake flux, which suggests that other processes than those accounted for by the model are operating, and ultimately driving nutrient acquisition. Nevertheless, sensitivity analyses conducted with such models (Barber 1995) showed for poorly mobile nutrients such as P that the major parameters were (i) root elongation rate and (ii) nutrient availability in the soil (concentration and buffer power), while the least important parameters were those describing the nutrient absorption capacities of the roots (Michaelis-Menten parameters). Rengel (1993) underlined that the uptake was thus not the limiting step of nutrient acquisition for poorly mobile nutrients such as K and P, contrary to water or the case of more mobile nutrients such as nitrate. In spite of this, it is quite astonishing to see so much excellent work concentrating on the identification of P transporters in plants.

Major challenges are in front of us for improving current models of plant nutrition and upscaling rhizosphere knowledge (Darrach et al. 2005; Dunbabin et al. 2006; Hinsinger et al. 2005 and 2008; Jones and Hinsinger 2008) given that reducing fertiliser inputs will require a better prediction of nutrient acquisition in nutrient-poor soils. At a biophysical point, two major improvements are needed. First of all, we need a better description of what is the actual surface of uptake to account for. So far, most models rely on a very poor description of root growth, and do not explicitly account for root architecture, although root architecture models as those developed by Lynch (Ge et al. 2000 ; Liao et al. 2001 ; Lynch

et Brown 2001 ; Rubio et al. 2003) have proved useful for describing situations of heterogeneous distribution of nutrients in the soil profile. Accounting for architecture is especially needed for the most mobile nutrients such as nitrate, as root-root competition and consequent overlapping of nutrient depletion zones is increasing with increasing diffusion coefficient (Ge et al. 2000 ; Hinsinger et al. 2005). While models of nutrient acquisition have been improved to account for root hairs which play a prominent role in extending the volume of P depletion zone (Gahoonia et al. 2001; Gahoonia et al. 2004 a and b), very little progress has been made to account for the contribution of mycorrhizal hyphae. This is amazing given that it is largely admitted that mycorrhizal symbiosis plays a key role in P acquisition by most plants (Smith et al. 2003), especially in low input conditions. Schnepf and Roose (2006) and Schnepf et al. (2008) have recently made steps forward to account for P depletion zones around mycorrhizal hyphae in a root segment model. This shall now be done at the more realistic scale of a whole root system model.

Another major improvement of nutrient acquisition models shall rely on a better coupling with water dynamics. Doussan and co-workers (Doussan et al. 1999, 2003 and 2006) have made major progress in modelling water uptake at the rhizosphere up to whole root system scales by explicitly accounting for root architecture and spatial heterogeneity of water uptake capacities along root axes. This, combined with the temporal and especially diurnal, patterns of water uptake generates complicated water gradients around roots, which should be accounted for as they ultimately govern the fluxes of nutrients as well. Finally other biophysical processes shall also be accounted for in a comprehensive model of rhizosphere functioning, such as those processes that are related to mechanical effects of root growth (both axial and radial) or the production of mucilage by either roots or rhizosphere microorganisms, and the subsequent formation of rhizosheaths (Hinsinger et al. 2009).

Rhizosphere biogeochemical processes

A major drawback of current models of nutrient acquisition is that they do not account for the biogeochemical processes which occur in the rhizosphere, as a consequence of either root or microbial activities (Marschner 1995; Hinsinger 1998; Hinsinger et al. 2005 and 2008), and which certainly explain the unexpected concentration gradients that one can frequently observe in the rhizosphere (e.g. Hinsinger and Gilkes 1996; Bravin et al. 2009). A few attempts have been made to account for the potential impact of root exudates such as carboxylic anions in the acquisition of P at the root segment scale (Geelhoed et al. 1999 ; Kirk et al. 1999). Such models hardly account for the several concurrent biogeochemical processes interacting with nutrient acquisition, especially so for P (Raghothama 1999 ; Hinsinger 2001 ; Vance et al. 2003; Raghothama and Karthikeyan 2005) and micronutrients. At best, they only account for a single rhizosphere process, e.g. citrate exudation (Geelhoed et al. 1999 ; Kirk et al. 1999), and the competitive desorption of phosphate by citrate (Geelhoed et al. 1999). They should account for additional rhizosphere processes such as pH changes and complexation of metal cations which have been shown to play a key role in determining P acquisition (e.g. Gerke et al. 2000 ; Hinsinger 2001) and iron (Fe) acquisition (Marschner 1995; Robin et al. 2008). The role of phytosiderophores in the complexation of Fe and other micronutrients such as Zn and Cu is well known as a

major strategy, as developed by Poaceae (Römheld and Marschner, 1985). Rhizosphere microbes are also known to be key players in the bioavailability of Fe, especially via the release of siderophores (Marschner 1995; Robin et al. 2008). The complexation of metals by root or microbial exudates is however depending on the pH, and the potential competition with other metal cations, of which concentrations can tremendously vary in the rhizosphere. Obviously, only reactive transport, multicomponent models as developed in geochemistry appear as suitable tools to better predict the fate of reactive nutrients such as P and micronutrients at the soil-root interface (Anoua et al. 1997; Nowack et al. 2006; Devau et al. 2008; Szegedi et al. 2008).

A number of the rhizosphere processes that have been cited above as key players in nutrient acquisition are regulated by the nutritional status of the plant itself: the root-induced release of protons or the exudation of carboxylic anions as well as enzymes such as phosphatases have been shown to be stimulated under P deficient conditions (Neumann and Römheld 1999; Raghothama 1999; Hinsinger 2001; Richardson et al. 2001; Vance et al. 2003; Tang et al. 2004; Raghothama and Karthikeyan 2005). Such feedback processes would need to be accounted for in future attempts to model nutrient acquisition. In addition, contrary to nutrient absorption, as for example for P (Rubio et al. 2004), many of those rhizosphere processes are not homogeneously distributed along root axes, which means again that a functional root architecture should be implemented in future models. Many works have shown that apical root zones were responsible for larger fluxes of exudates or protons (Neumann et al. 1999; Hinsinger et al. 2003; Vansuyt et al. 2003; Lambers et al. 2006). This is especially documented for protons in strategy I plant species which exhibit enhanced proton efflux behind root apices as a response to Fe deficiency (Marschner 1995; Hinsinger et al. 2003; Vansuyt et al. 2003). The enhanced secretion of phytosiderophores in strategy II plant species (Poaceae) as a response to Fe deficiency is also known to have a rather constrained spatial and temporal pattern. These shall be accounted for when predicting Fe acquisition by Poaceae, as suggested by Darrah (1991) for root exudates. The work of Dunbabin et al. (2006) which accounted for the increased availability of rhizosphere P as a consequence of the exudation of surfactants (phospholipids) has led to major advances in rhizosphere modelling. It showed that it is worth upscaling at the whole root system scale in order to account for the feedback effects of improved plant P nutrition on root growth and further extension of the prospected soil volume, ultimately increasing P acquisition. Dunbabin et al. (2006) calculated in a high P soil that the extra benefit of the exudation of surfactants on P acquisition was rather negligible at the root segment scale (only 4% increase), while it became significant at the whole root system scale (about 13%). In a low P soil, the extra benefit was obviously much larger, close to 50% increase in P acquisition, at the whole root system scale.

Rhizodeposition is a key biogeochemical process occurring in the rhizosphere (Hinsinger et al. 2005 and 2009; Jones et al. 2009). Besides the direct implication of root exudates in the mobilisation of specific nutrients, this process can have a considerable impact on the acquisition of nutrients via the stimulation of microorganisms in the rhizosphere. Raynaud et al. (2006) recently showed that the whole microbial loop could be modelled to better describe the fate of N in the rhizosphere. These authors accounted for the stimulation of

microorganisms and also for predation of rhizosphere bacteria by the fauna (protozoa or nematodes) which is known to play a significant role in delivering extra N (Griffiths 1994).

Our knowledge of the biogeochemical processes governing nutrient acquisition has considerably increased over the last decades (Hinsinger et al. 2009), and is currently much more advanced than for biophysical processes. How to make use of the accumulated knowledge on rhizosphere biophysics and biogeochemistry to face the issue of ecological intensification of agroecosystems, and especially that of improving N and P efficiencies and micronutrient fortification in plants ?

Conclusions – What could be new routes for ecological intensification of agroecosystems ?

The perspectives for further intensification of agroecosystems based on a better use of genetic resources are limited, given that the ceiling of yield potential is close to be reached by now (Wissuwa et al. 2009). Plant breeding has essentially been conducted in non limiting environments, thereby leading to the selection of highly productive genotypes under high fertiliser input conditions, while leaving aside rustic genotypes which may be better adapted to low input conditions (Dawson et al. 2008). This has ultimately led to a considerable impoverishment of the genetic diversity in commercial varieties of most crop species (Khush 2001 ; Rengel et Marschner 2005). We thus need to fully revise the breeding schemes to account for new criteria such as soil N or P use efficiency in low input agroecosystems (Tilman 1999 ; Rengel and Marschner 2005 ; Ismail et al. 2007 ; Lynch 2007 ; Wissuwa et al. 2008). As pointed out by Lynch (2007), the ‘roots of the second Green Revolution’ rely on better accounting for root traits and soil-root-microbe interactions that occur in the rhizosphere (Wissuwa 2003 and 2005; Wissuwa et al. 2009). However, even if including such new traits, we may still have it all wrong pursuing the quest of the champion genotype of each of our crops.

Progress is rather expected in terms of increased yield stability, hence phenotypic plasticity, and sustainability, via increased use efficiency of soil resources (Tilman et al. 2002). For this purpose, the development of an ecological engineering of agroecosystems is a promising alternative, which shall take its inspiration from the understanding of natural ecosystems. A major difference between intensive agroecosystems and natural ecosystems is biodiversity, especially so at the level of plant community. While most natural ecosystems are made of complex assemblages of plant species, agroecosystems are characterised by extremely simple plant communities, most often a single species and a single variety in a field. A better nutrient use efficiency shall be expected from more diverse systems, either pluri-specific such as intercropping or agroforestry systems, where niche complementarity and facilitation occur (Tilman et al. 2002 ; Li et al. 2007 and 2008). Such complex systems only start being modelled to account for rhizosphere facilitation processes (e.g. Raynaud et al. 2008).

For N, it is rather astonishing how symbiotic N₂ fixation in legumes is underused in intensive agroecosystems (Rengel 2002). The N benefit for the plant species intercropped

with legumes relies on several complex rhizosphere processes that are being now well understood (Jensen 1996; Hauggaard-Nielsen and Jensen 2005; Høgh-Jensen 2006; Rasmussen et al. 2007; Wichern et al. 2007). Besides making better use of symbiotic N₂ fixation, increasing soil N use efficiency should be done while minimising losses of N as nitrate or N oxides. For such purpose, innovative strategies must be promoted instead of current practices which are mostly based on the assumption that nitrate is the sole pool of soil N which is available to crops (Giles 2005 ; Subbarao et al. 2006). The ability of plants to mobilise N forms that are produced prior to nitrate along organic matter mineralisation, such as ammonium or even aminoacids would be worth being better exploited (Lipson et al., 1999; Falkengren-Grerup et al., 2000; Glass 2003). It seems now possible to mimic natural ecosystems where certain N-efficient grasses have been reported to produce nitrification inhibitors (Lata et al. 2004). Subbarao et al. (2007), pursuing this strategy have shown that exudation of nitrification inhibitors was observed in a whole range of species, including sorghum and peanut. In addition, better exploiting other rhizosphere processes such as associative N₂ fixation by diazotroph rhizobacteria (e.g. *Azospirillum brasilense*) is another means worth being pursued, in the light of cereal-based agroecosystems of Mexico or Brasil, especially sugarcane production (Baldani et al. 2002 ; Boddey et al. 2003).

For P, there are many potential options for increasing acquisition efficiency in crop species (Raghothama 1999 ; Hinsinger 2001 ; Vance et al. 2003; Raghothama et Karthikeyan 2005 ; Lambers et al. 2006 ; Ismail et al. 2007), and Lambers et al. (2006) stressed that we should have a closer look at how wild species cope with low availability of P in poor soils to design new strategies. These could be based on root traits that relate to rhizosphere biophysics, such as root architecture, root hairs (Ge et al. 2000 ; Gahoonia et al. 2001 ; Lynch and Brown 2001 ; Rubio et al. 2003 ; Wissuwa 2003 and 2005; Gahoonia et Nielsen 2004a et b ; Lynch 2007). Alternative strategies could rely on root traits that relate to rhizosphere biogeochemistry, via the physiology of plant roots (exudation of protons, carboxylates or phosphatase enzymes ; Neumann et Römheld 1999 ; Hinsinger 2001 ; Richardson et al. 2001; Vance et al. 2003 ; Wissuwa 2003 and 2005 ; Tang et al. 2004 ; Yan et al. 2004 ; Raghothama et Karthikeyan 2005). Other potential strategies could exploit traits related to the physiology of associated microorganisms, either symbiotic such as mycorrhizal fungi (Hettrick et al.1993 et 1996 ; Zhu et al. 2001), or P-solubilising bacteria and fungi (Marschner et al. 2006). There are many ‘tricks’ and possible routes, but contrary to much of the past research, following more than a single one maybe the best way not to get lost !

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