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5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

K-3

Soil-Root-Microbe Interactions in the Rhizosphere - A Key to Understanding and Predicting Nutrient Bioavailability to Plants

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Introduction – Why shall we care about nutrient bioavailability to plants?

As stressed in the Millennium Ecosystem Assessment, 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 much contributed to improving humankind well-being, but this was achieved at the expense of a degradation of numerous ecosystem services and increasing poverty of the poorest populations. Prediction models forecast further degradation of ecosystem services in the coming 50 years, *a fortiori* if agroecosystem management strategies are unchanged (Tilman et al. 2001 et 2002). In this context, Millennium Development Goals will hardly be achieved, and especially the very first of these: to eradicate hunger worldwide (Priority 1). The scientific challenge is considerable: how to feed the world in a context of limited changes of land use, i.e. a limited increase in productive arable land surface area?

As pointed out by Vance et al. (2003), by 2030, world population shall have increased by about +33 to +67%, while in the mean time, the potential increase in surface area of arable land will reach at most +20%, and that of irrigated land less than +10%. Given the climate changes which operate and the increasing use of arable land for other uses than food production, the challenge in front of us is even bigger (Tilman et al. 2002). The level in agriculture productivity needs to be maintained or further increased, but this has to be achieved in a sustainable manner, both environmentally and economically, in order to preserve ecosystem services. There is 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) and contamination of groundwaters by nitrate. These phenomena are the direct consequence of the considerable increase in agricultural inputs and the steady decrease of their efficiency (Tilman et al. 2002) : from 1965 to 2000, the doubling of the production of world agriculture concurred with a 3.5- and 6.9-fold increase in the amounts of P and N fertilisers applied, respectively (Tilman 1999). Besides the effects of eutrophication and of nitrate in drinking water, the high and fast-increasing cost of energy and thus that of manufactured N fertilisers, as well as the negative impacts of greenhouse gas emissions invalidate the perspective of pursuing the current, steady increase in N fertiliser application. For P, the fast exhaustion of



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

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 fertilizer use in developed countries.

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 this purpose, one needs to better know what are the intimate processes and factors that govern soil nutrient bioavailability to plants. The aim of this review is to address this issue, with a particular focus on those soil-root-microbe interactions at play in the rhizosphere.

Revising the concept of bioavailability to plants – a rhizosphere perspective

Bioavailability is a widely used concept, although poorly defined by most of its users, in various scientific communities such as agronomy, ecology, ecotoxicology, food and medical sciences. Initially used for nutrients, this term is nowadays largely used for chemicals, e.g. inorganic or organic pollutants in the context of ecotoxicology. As stressed by Harmsen et al. (2005), many of the definitions are rather loose and do not explicitly state how strongly the bioavailability relies on the target organism and time. For instance, Thornton (1999)'s definition stated that is '*bioavailable that fraction of an element present in soil which is available for intake into plant roots or into soil microorganisms and other flora and fauna*', which is parallel to the concept developed in toxicology or medical science, stating that it corresponds to '*that fraction in the soil, dust or diet that is bio-accessible (e.g. soluble and available for uptake in the gastro-intestinal tract of animal, including farm livestock and humans)*'. Although this definition suggests that the bioavailability of a soil nutrient varies with the target organism, it does not provide any indication of the time frame, as one needs when moving from a conceptual definition towards a more operational definition. At this point of view, one may prefer the following definition: *the bioavailability is the amount of a nutrient in the soil that is present in forms that plants (or other organisms) can take up during the time that they are growing*. In other words, and as stressed by the ISO (2008), bioavailability is best defined as a flux or rate of uptake of a nutrient by the plant.

Harmsen et al. (2005) and the working group which led to the ISO (2008) document on bioavailability also stressed that one should make a clear distinction between availability (or environmental availability) and bioavailability (or environmental bioavailability). Since the end of the nineteenth century, agronomists have been attempting to design chemical tools to assess the availability of nutrients in soils, some of which having been initially designed to mimick what plant roots were doing to acquire plant nutrients. In Europe only, there are for instance 17 soil test procedures that are currently being used for estimating P availability (Tunney et al. 1997), which is a clear indication that none is quite satisfactory to predict the bioavailability of P to crops. Of concern is the fact that many of the designers of these methods and an even larger proportion of their users take the easy (but wrong) shortcut, pretending that they provide a measurement of the bioavailability. They are to be considered at best as a surrogate, a practical way of estimating the bioavailability. But it shall be stressed that chemical methods cannot measure the bioavailability of a nutrient in a soil because by definition, the bioavailability is expected to vary depending on the organism that is targeted.



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

In other words, contrary to the availability for a given soil and a given nutrient, there are different bioavailabilities depending of the target organism. As pointed by Harmsen et al. (2006) and ISO (2008), as a follow up on the former work of Lanno et al. (2004), this is largely due to the fact that for each considered organism, a so-called 'bio-influenced zone' can be defined, which is the portion of the environment with which an organism interact. In this zone, which typically corresponds to the rhizosphere in the case of plants, the physiological activities of the organism results in changes of those soil parameters and processes that determine the availability of a nutrient, e.g. a change in pH or the release of an exo-enzyme such as phosphatase for instance. Thus, the bioavailability of nutrients will depend on how much each organism is capable to alter the availability of nutrients in his 'bio-influenced zone'. For the case of plants, one may expect considerable variations in bioavailability of nutrients from one species to another, or even from one genotype to another within a single species, depending on its ability to alter rhizosphere processes and properties (see for example for P, Horst et al. 1996; Hinsinger 2001; Li et al. 2008).

Rhizosphere biophysics

The bioavailability being defined as a flux of nutrients that can be taken up by the roots of a given plant genotype, it is rather straightforward that processes implied in the transfer of nutrients towards the root surface, and ultimately their uptake into root cells must be accounted for. This is well illustrated by the Barber (1995) modeling approach of bioavailability. Transfer processes that play a key role in that respect are mass-flow and diffusion, the relative contribution of each varying from a nutrient to another, depending also on the plant requirements and the availability of the nutrient in the soil, especially its concentration in the soil solution. Actually 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: beside the concentration of the nutrient in soil solution, they also accounted for the buffering capacity of the soil, i.e. the ability of the soil to replenish soil solution when depleted as a consequence of nutrient uptake. In such models and in the many nutrient uptake models that have been deriving since then, the central hypothesis is that the driving force of nutrient bioavailability it the absorption process which results in a decrease of the nutrient at the surface of the root, leading to a diffusion gradient in the rhizosphere. This is supported by ample of experimental evidence for nutrient depletion occurring in the rhizosphere, and 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 contributes rather little to the transfer towards the root surface as K and P usually occur at rather low concentrations in the soil solution. Mass-flow becomes more important for those nutrients that occur in larger concentrations in the soil solution, typically for calcium (Ca) and magnesium (Mg) among cations: their transfer by mass-flow can even be larger than plant requirements, thereby resulting in an increase in their concentration in the rhizosphere. Mass-flow can also contribute a significant proportion on nitrate transfer towards the root surface, but depletion is expected to occur because of the large N requirements of plants. There has been some reports of more complex patterns of nutrient distribution in the



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

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). Such complex patterns can hardly be accounted for by the classical model of nutrient bioavailability of Barber (1995).

Further refinements of the Nye and Mariott (1969) derived models consisted to upscale from the root segment to the whole plant (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 bioavailability to crops over time scales of days or weeks in the case of soils exhibiting high K or P availability, but they failed in limiting conditions (Brewster et al. 1976; Schenk and Barber 1980; Lu and Miller 1994; Mollier et al. 2008). In soils exhibiting low K or P availability, those models systematically underestimate the actual uptake flux, which suggest other processes than those accounted for by the model are operating, and ultimately driving nutrient bioavailability. Nevertheless, sensitivity analyses conducted with such models (Barber 1995) showed for poorly mobile nutrients such as P (and K) 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 (Michealis-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.

Major challenges are in front of us for improving current models of plant nutrition and upscaling rhizosphere knowledge (Darrah et al. 2005; Dunbabin et al. 2006; Hinsinger et al. 2005 and 2008; Jones and Hinsinger 2008) given that reducing fertiliser inputs needs better predicting the bioavailability of nutrients in nutrient-poor soils. At a biophysical point of view, a better prediction of nutrient bioavailability would need two major of improvements. First of all, as long as the bioavailability is defined as a flux, it is needed to better describe what the actual surface of uptake to account for is. 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 the initial models of nutrient bioavailability have been improved to account for root hairs which play a prominent role in extending the volume of the depletion zone for poorly mobile nutrients such as P (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 contradicts the largely admitted view of the key role of mycorrhizal symbiosis in determining P bioavailability to most plants (Smith et al. 2003), especially in soils exhibiting low P availability. Schnepf and Roose (2006) have recently made a first attempt to account for P depletion zones around mycorrhizal hyphae in a root segment model.



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

This shall be done at the more realistic scale of a root system model of plant nutrition and may have implications for predicting the bioavailability of P and also other nutrients such as N, K, zinc (Zn) or copper (Cu), for which a significant contribution of mycorrhizae has been shown in the literature.

Another major improvement of nutrient bioavailability models shall rely on a better coupling with water dynamics. Doussan and co-workers (Doussan et al. 1998, 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 (fluxes) along root axes. This, combined with the temporal and especially diurnal, patterns of water uptake generates complicated water content distribution patterns 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 the roots of rhizosphere microorganisms, and the subsequent formation of rhizosheaths (Hinsinger et al. 2008).

Rhizosphere biogeochemistry

Another major drawback of current models of nutrient bioavailability is that they do not account for the many biogeochemical processes that have been shown to occur in the rhizosphere, as a consequence of either root or microbial activities (Marschner 1995; Hinsinger 1998; Hinsinger et al. 2005 and 2008). 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 many concurrent biogeochemical processes that interact with nutrient bioavailability, 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 function (citrate exudation for instance, Geelhoed et al. 1999; Kirk et al. 1999) and its interaction with P availability (competitive desorption of phosphate ions by citrate for instance, Geelhoed et al. 1999). They should *a minima* account for additional rhizosphere processes such as pH changes and complexation which have been shown to play a key role in determining P bioavailability (e.g. Gerke et al. 2000; Hinsinger 2001) and iron (Fe) bioavailability (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 Gramineous plant species (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 the many 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



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

bioavailability of reactive nutrients such as P and micronutrients in soils (Anoua et al. 1997; Nowack et al. 2006; Devau et al. 2008; Szegedi et al. 2008).

A number of the rhizosphere functions that have been cited above as key players in nutrient bioavailability 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 bioavailability. In addition, contrary to the function of nutrient absorption, as for example for P (Rubio et al. 2004), many of those rhizosphere functions 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 (Graminaceous species) as a response to Fe deficiency is also known to have a rather constrained spatial and temporal pattern. They are released at greater flux at the root tips and between 3 and 6 hours after the onset of light in the morning. These patterns shall be accounted for when modelling soil Fe bioavailability to Graminaceous plants, as suggested by Darrah (1991) for other 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 was worth up-scaling at the whole root system scale in order to account for feedback effects of improved P bioavailability on root growth and further extension of the prospected soil volume, ultimately increasing the amount of P acquired. Dunbabin et al. (2006) calculated in a soil exhibiting a high P availability that the extra benefit of the exudation of surfactants on P uptake 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 soil exhibiting a low P availability, the extra benefit was obviously much larger, close to 50% increase in P bioavailability, at the whole root system scale.

Rhizodeposition is a key biogeochemical process occurring in the rhizosphere (Hinsinger et al. 2005 and 2008; Jones et al. 2008). Besides the direct implication of root exudates in the mobilization of specific nutrients, this process can have a considerable impact on the bioavailability 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 bioavailability 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).



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

While our knowledge of the various biogeochemical processes that may influence nutrient bioavailability has considerably increased over the last decades, as reviewed by Hinsinger et al. (2008), and is now much more advanced than for biophysical processes, there is still a need to put all this knowledge together.

Conclusions – what is the way forward?

A central question is how to make use of the accumulated knowledge on nutrient bioavailability to face the issue of ecological intensification of agroecosystems, and especially that of improving N and P efficiencies and micronutrient fortification in plants.

The perspectives for further intensification of cropping systems based on a better knowledge and valorization of genetic resources are nevertheless limited in terms of increased productivity, given that the ceiling of yield potential is considered to be close to be reached by now (Wissuwa et al. 2008); progress is to expected rather at the level of an increased stability and sustainability, via increased use efficiency of soil resources such as water, N and P for instance (Tilman et al. 2002). For this purpose, the development of an ecological engineering of agrosystems is promising, which shall take its inspiration from the understanding of natural ecosystems. A major difference between intensive agrosystems 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, agrosystems are characterized 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 (Tilman et al. 2002; Li et al. 2007 and 2008). Such complex systems only start being modelled (e.g. Raynaud et al. 2008).

Plant breeding has essentially been conducted in non limiting environments, thereby leading to the selection of highly productive genotypes under conditions of heavy use of fertilisers, 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 and Marschner 2005). It is thus now necessary to fully revise the breeding schemes in order to take into account new criteria such as soil N or P use efficiency in low input growing conditions (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. 2008).

For N, it is most relevant to better valorize symbiotic N₂ fixation in legumes by giving a more prominent position of legumes in cropping systems, either in rotation, or intercropped with cereals or other crops (Rengel 2002). As far as cereals are concerned, the aim should be to increase soil N use efficiency while minimising losses of N as nitrate (leaching and groundwater pollution) or N oxides (greenhouse gas emission). 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 bioavailable to crops (Giles 2005 ;



5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

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). Rather than applying synthetic nitrification inhibitors, it seems now possible to mimic natural ecosystems where certain grasses have been reported to produce such compounds (Lata et al. 2004). Subbarao et al. (2007) have adopted such a strategy and shown that exudation of nitrification inhibitors by roots was observed in a whole range of plant species, including crops such as sorghum (*Sorghum bicolor* L.) or peanut (*Arachis hypogea* L.). 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 systems 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), either based on root traits (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), or rhizosphere traits related to 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) or the physiology of associated microorganisms, symbiotic such as mycorrhizal fungi (Hettrick et al.1993 et 1996 ; Zhu et al. 2001), or not such as P-solubilising bacteria and fungi (Marschner et al. 2006).

Keywords: Rhizosphere; soil-root-microbe interactions; nutrient bioavailability.

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5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

Keynote papers

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5th International Symposium ISMOM 2008 - November 24th - 28th, 2008 - Pucón, Chile

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