

# P for Two, Sharing a Scarce Resource: Soil Phosphorus Acquisition in the Rhizosphere of Intercropped Species<sup>1</sup>

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Over the last 50 years, the use of nitrogen (N) and phosphorus (P) fertilizers has increased at a faster rate than global food production, resulting in substantial decreases of N and P efficiency in agriculture (Fig. 1). Thus, considerable amounts of N and P fertilizers have been wasted in agroecosystems, and the alteration of N and P biogeochemical cycles is among the most visible impacts of human activities on ecosystem services, far exceeding the hypothesized “planetary boundaries” for N and approaching those for P (Rockström et al., 2009). Projections for the future suggest that a substantial further increase in N and P fertilizer use will occur to cope with increasing food demand (Tilman et al., 2001; Vance et al., 2003). Tilman et al. (2001) predicted that global consumption of fertilizer P will increase from 34.3 Tg year<sup>-1</sup> in 2000 to a mean projected value of 83.7 Tg year<sup>-1</sup> in 2050 (56.2–118 Tg year<sup>-1</sup> depending on the calculation scenario). Such increases in fertilizer consumption will further threaten the global N and P cycles. Bouwman et al. (2009) estimated that in 2000, the total input of fertilizer P in croplands amounted to 21 Tg year<sup>-1</sup>, of which 9 Tg was accumulated in soils and 1 Tg was lost to erosion. Their projections for 2050 for various scenarios of future agricultural development amounted to 29 to 46 Tg year<sup>-1</sup> total P fertilizer input and 10 to 23 and 3 to 5 Tg year<sup>-1</sup> accumulated in soil and lost to erosion, respectively. This suggests that even in the most optimistic scenario, the contribution of P fertilization of cropland to P movement by erosion will triple over the period 2000 to 2050. While further intensification of agroecosystems is clearly needed to cover the growing food demand over the next decades, we cannot afford to accept the “business as usual” scenario that relies on ever-increasing agricultural inputs and the resulting waste of nutrients in some regions of the world (Vitousek et al., 2009).

## WHAT MAKES P SO SPECIAL?

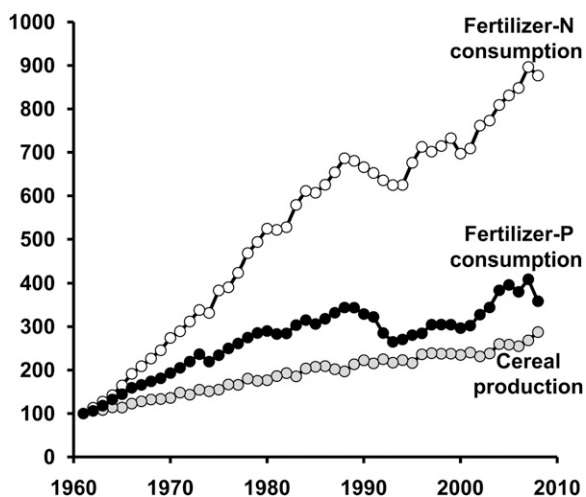
Contrary to N, P is reasonably abundant in the Earth's crust (1.2 g kg<sup>-1</sup> on average) and thus in soils, where it primarily occurs as inorganic P in apatite minerals derived from the bedrock. However, with soil formation and weathering, total P content decreases over time and organic P content builds up at the expense of inorganic P, as shown in soil chronosequences (Richardson et al., 2004). At early stages of development (in young soils), therefore, terrestrial ecosystems are primarily N limited, while at later stages of development (in older soils), they become P limited (Vitousek and Farrington, 1997). Thus, soil P scarcity is especially critical in the tropics, where deeply weathered soils dominate. In addition, unlike N (especially nitrate), phosphate ions are poorly mobile and present at low concentration in soil solution, due to strong and multiple interactions with soil constituents (Hinsinger, 2001). These comprise adsorption onto soil minerals (metal oxides and clay minerals), precipitation as P minerals (predominantly apatite-like minerals), and immobilization as various organic P compounds (soil organic matter and phytate, which is the P storage form in seeds). P limitation is thus widespread, estimated to affect about 5.7 billion ha worldwide (Gaume, 2000).

While, in spite of their considerable energy cost, the reservoir of atmospheric N<sub>2</sub> used for manufacturing N fertilizers is much larger than required, the situation for P is rather different. World reserves of P ores are indeed finite, and the exact time when their consumption will peak is a matter for debate. High-grade phosphate rocks are definitely expected to be exhausted within the next decades (Cordell et al., 2009), which calls into question the sustainability of current P fertilizer use in developed and emerging countries. Increasing P efficiency in crops without further increasing P inputs requires better exploration and exploitation of soil resources in agroecosystems. To achieve this, we must breed more P-efficient crop genotypes that will make better use of belowground (root architecture and rhizosphere-related) traits (Vance et al., 2003; Lynch, 2007). Another promising option for achieving ecological intensification of agroecosystems (Cassman, 1999) is to make better use of plant diversity, especially niche complementarity and facilitation occurring in the rhizospheres of intercropped species (Zhang et al., 2010).

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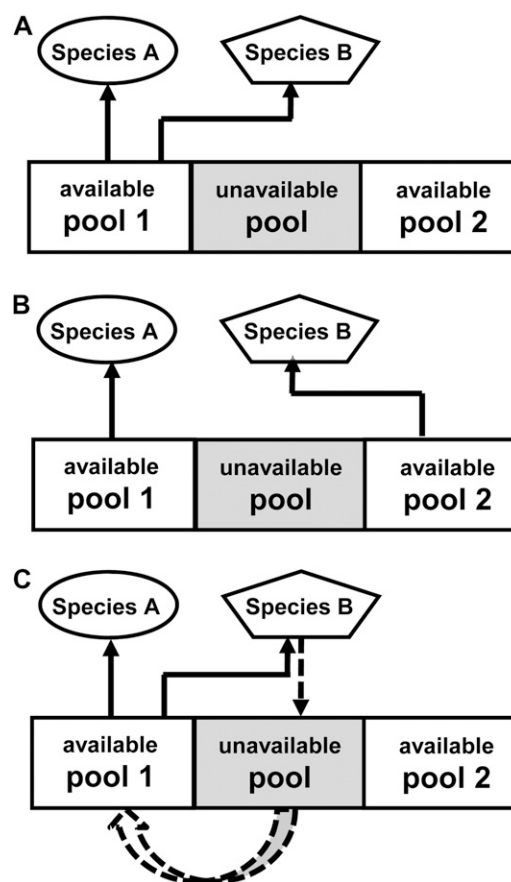
**Figure 1.** Relative increase in world annual production of cereals, and global annual consumption of fertilizer N and fertilizer P over the period from 1961 to 2008. The 100-basis in 1961 corresponds to 876.9 Tg cereals year<sup>-1</sup>, 11.6 Tg fertilizer N year<sup>-1</sup>, and 4.8 Tg fertilizer P year<sup>-1</sup>. In 2008, these values were 2,520.7 Tg cereals year<sup>-1</sup>, 101.6 Tg fertilizer N year<sup>-1</sup>, and 17.1 Tg fertilizer P year<sup>-1</sup>. (Data are from FAOSTAT [http://faostat.fao.org/], accessed February 20, 2011).

#### BETTER EXPLOITING PLANT FUNCTIONAL DIVERSITY IN CROP-BASED AGROECOSYSTEMS: THE CASE OF CEREAL/LEGUME INTERCROPS

Enhanced productivity of multispecies agroecosystems (intercropping) compared with that of monospecific agroecosystems (each of the component species being grown alone) may be explained by two major processes that result in improved resource use: complementarity and facilitation (Fridley, 2001). Experimentally, these processes can be difficult to tease apart (Loreau and Hector, 2001). Complementarity may be defined as a decrease in interspecific competition and competitive exclusion through resource partitioning between intercropped species (Fig. 2). Species may use a given resource differently in time, in space, and in forms (Fridley, 2001). A well-known example is the complementarity of N use between cereals and N<sub>2</sub>-fixing legumes, where both species compete for the same pool of soil N, while only the legume can substantially access the additional pool of atmospheric N<sub>2</sub> through symbiotic fixation. Facilitation occurs when one species enhances the growth or survival of another (Callaway, 1995). This can occur through (1) direct positive mechanisms, such as favorable alteration of light, temperature, soil moisture, soil nutrients, etc., and (2) indirect mechanisms, such as beneficial changes in soil mycorrhizal or microbial communities. Hereafter, we use facilitation to mean positive interactions by which a species can modify the biotic/abiotic environment of its roots (rhizosphere), ultimately benefitting the intercropped species by increasing nutrient availability (Callaway, 2007). Direct, root-mediated processes altering P availability in the

rhizosphere and indirect, microbially mediated processes will be addressed.

Such positive interactions are particularly valuable when resources are limited, as occurs in low-input agroecosystems. For example, beneficial effects of intercropping have been observed at lower rates of P fertilizer application but were no longer significant at higher rates (Li et al., 2007). In ecology, the “stress gradient hypothesis” proposes that positive interactions (facilitation) increase in importance and intensity with increasing environmental stress (Brooker et al., 2005). For both natural and managed ecosystems, nutrient use in multispecies stands has been mainly studied for N and especially for cereal/legume intercropping systems. Few studies have focused on cereal-legume interactions with regard to soil P. Recently, this research field has attracted new interest with the reported evidence of



**Figure 2.** Competition (A), complementarity (resource use partitioning; B), and facilitation (C) between two intercropped species. Pools represent different forms of a single resource (e.g. nutrient). Solid arrows indicate uptake of the resource by the intercropped species, while dotted arrows indicate mechanisms by which species B can alter resource availability, increasing the size of the available pool at the expense of the unavailable pool (indicated by the curved arrow), thereby improving uptake of the resource by the intercropped species A (facilitation).

enhanced P acquisition for cereals intercropped with legumes (Li et al., 2007).

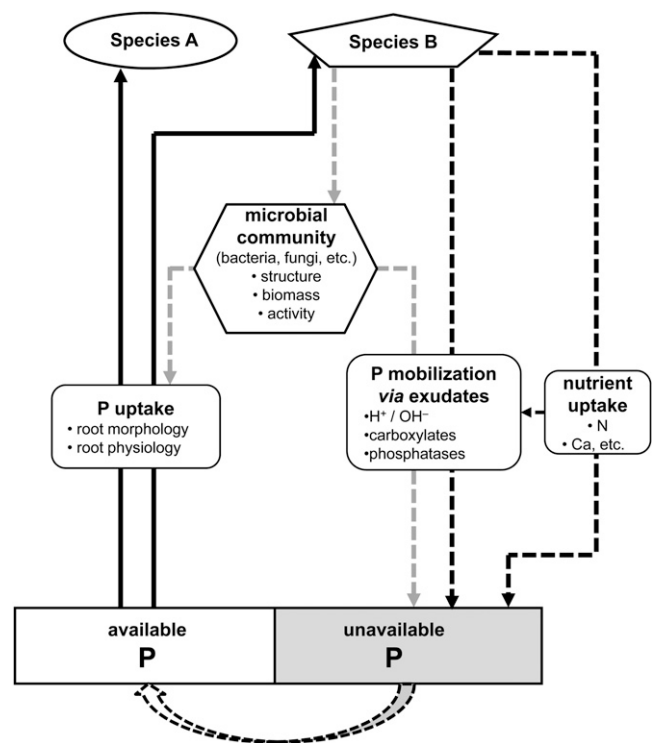
### COMPLEMENTARITY IN SPACE, TIME, AND SOIL P POOLS

Given the low mobility of phosphate ions in soils, the volume and geometry of the rhizosphere largely determines the pool of P readily accessible to plants. Spatial complementarity can occur (1) when the two species have contrasting root architecture, exploring different soil horizons, and/or (2) because of the plasticity of root systems, combined with possible avoidance strategies (Hauggaard-Nielsen and Jensen, 2005; Li et al., 2006; de Kroon, 2007). In both cases, intercropping may ultimately result in better exploration of the whole soil volume compared with monocropping. The role of root distribution in resource use in intercropping systems has been mostly documented for N. But the conclusion that cereal has better N uptake efficiency due to faster root growth may also apply to P. The discovery that plants can adjust root location depending on nutrient availability and the presence of neighboring plants within a single species (Gersani et al., 2001; Cahill et al., 2010) raises new questions about how soil P is shared in multispecies stands and how "root decisions" (Hodge, 2009) occur for intercropped species. In addition, intercropped species may exhibit contrasting phenologies (Rose et al., 2007) and/or growth periods (e.g. different sowing dates), which may result in differential P requirements over time (Li et al., 1999, 2007). Contrasted sowing/harvest dates may also reduce competition and increase P availability by mineralization of crop residue, which enhances P acquisition of the intercropping system.

Soil P occurs as various pools that require different biochemical or chemical reactions to release phosphate ions that are readily taken up by roots. Complementarity can thus occur for two intercropped species tapping into two distinct pools of soil P resources (e.g. inorganic and organic; Li et al., 2008). Intercropped species may also have access to different fractions of each of these pools (Turner, 2008). Cu et al. (2005) observed that wheat (*Triticum aestivum*) and intercropped white lupin (*Lupinus albus*) depleted two distinct inorganic P fractions. In Li et al. (2003a), chickpea (*Cicer arietinum*) mobilized soil organic P and left more inorganic P available to the intercropped wheat. Li et al. (2008) tested this hypothesis on a larger number of inorganic and organic P fractions for durum wheat (*Triticum durum*) and common bean (*Phaseolus vulgaris*). Almost all values of soil P pools in the rhizosphere of the two intercropped species were intermediate between those in the monocropped cereal or legume. As for Cu et al. (2005), the rhizospheres of the intercropped species were not dissociated to measure the changes in P fractions separately for each of the intercropped species.

### DIRECT POSITIVE RHIZOSPHERE INTERACTIONS

Facilitation of P uptake is defined as the positive interactions that result from the ability of one species to increase soil P availability to the benefit of the intercropped species (Callaway, 2007). Thus, for example, the size of the pool of available P is increased at the expense of the pool that is unavailable to species A (Figs. 2C and 3) as a consequence of exudation by species B. This section will focus on how plant roots are able to directly change rhizosphere P availability through either P uptake and exudation of P-mobilizing compounds or as a consequence of interactions with the uptake of other nutrients (Hinsinger, 2001; Vance et al., 2003; Devau et al., 2010). Root exudates play a major role in P bioavailability via several mechanisms: protons/hydroxyls and carboxylates solubilize inorganic P, while root-borne phosphatases hydrolyze organic P (Hinsinger, 2001; Vance et al., 2003). Most cereal/legume intercropping studies implicitly assume that the cereal shall benefit from the legume species (one-way facilitation), because legumes are known to excrete larger amounts of protons (Tang et al., 1997; Hinsinger



**Figure 3.** Root-induced (direct) and microbially mediated (indirect) positive interactions (facilitation) altering P availability in the rhizosphere of two intercropped species. Dotted arrows indicate how species B can mobilize P that is initially not available to species A, either directly (black arrows) or indirectly via soil microorganisms (gray arrows) such as bacteria and fungi, mycorrhizal or not. These processes result in increases in the size of the available P pool at the expense of the unavailable pool (indicated by the curved arrow). Solid black arrows indicate P uptake by the two species from the available P pool.

et al., 2003), carboxylates (Neumann and Römheld, 1999; Vance et al., 2003; Pearse et al., 2006), and phosphatases (Nuruzzaman et al., 2006) in their rhizosphere. But cereals can also change rhizosphere P availability, and one could well expect the facilitation of legume P acquisition by P-efficient cereals or even two-way facilitation in intercropped cereal/legume systems.

N uptake and the source of N used (ammonium, nitrate,  $N_2$ ) are known to play a key role in cation-anion uptake balance and subsequent changes in rhizosphere pH and P availability (Hinsinger et al., 2003). The intercropped cereal will presumably benefit from legume-mediated acidification due to  $N_2$  fixation in alkaline/neutral soils, where such acidification may increase P availability through dissolution of P minerals (Hinsinger, 2001). Several experiments have shown a lower rhizosphere pH in legumes than cereals, while rhizosphere pH of the intercropped cereal/legume is intermediate (Li et al., 2003a, 2008; Cu et al., 2005). However, none has established a causal relationship with plant performance. Li et al. (2008) reported a significant yield benefit when durum wheat was intercropped with common bean, relative to durum wheat grown alone, but they could not demonstrate the link with the observed changes of rhizosphere pH and acid-soluble P pools. These researchers, however, did show that proton release rate by the intercropped legume was significantly greater than that measured when the legume was grown alone. This likely occurred as a result of greater legume  $N_2$  fixation due to lower rhizosphere nitrate concentrations because of competition for soil N with the intercropped cereal, as documented elsewhere (Hauggaard-Nielsen et al., 2009). Indeed, when cropped alone, legumes tend to rely more on soil N when it is readily available due to the inhibiting effect of elevated nitrate concentration on  $N_2$  fixation. This provides an interesting case where competition for one resource (nitrate N) may stimulate facilitation for the acquisition of another resource (acid-soluble P).

Not only proton excretion but also hydroxyl release and subsequent increase in rhizosphere pH can substantially increase soil P availability. This occurs as a consequence of enhanced desorption of phosphate ions and changes in surface charges of iron oxides and clay minerals to which phosphate ions are bound (Hinsinger, 2001). Devau et al. (2010) both measured and modeled the substantial contribution of root-induced alkalization of the durum wheat rhizosphere to observed increases in P availability. These results were documented in a neutral soil but should occur for a broad range of soil types and initial pH values, provided that P availability is primarily constrained by adsorption/desorption processes. These findings suggest that cereals, which often exhibit improved N nutrition when intercropped (Bedoussac and Justes, 2010), may facilitate P acquisition by the intercropped legume.

Carboxylates and other organic ligands exuded by roots can compete with phosphate ions for adsorption on charged surfaces, thereby inducing ligand exchange-promoted P desorption and enhanced P availability

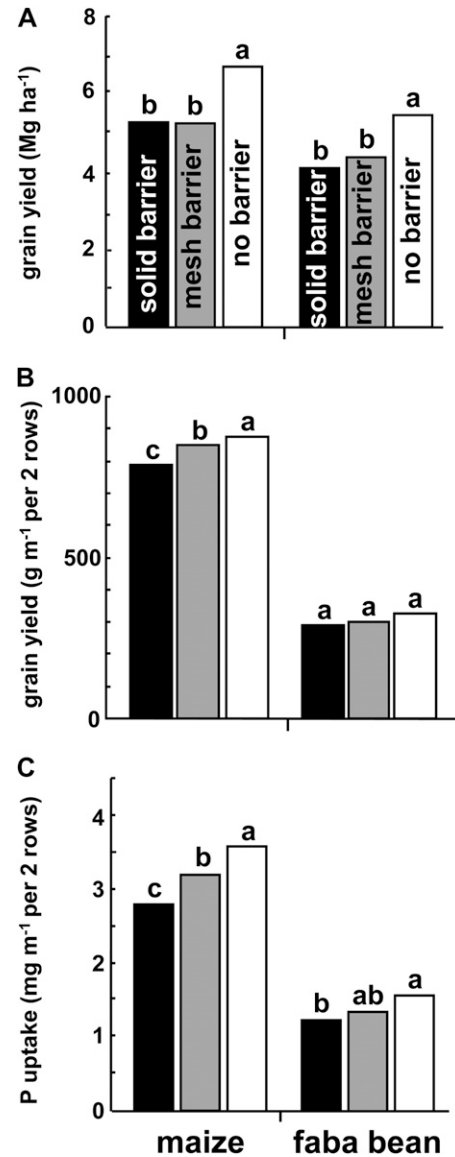
(Hinsinger, 2001). Carboxylate exudation rates are promoted under P-deficient conditions and vary considerably with plant species (Neumann and Römheld, 1999; Neumann and Martinoia, 2002; Vance et al., 2003), being much smaller in cereals than in certain grain legumes such as chickpea and white lupin (Neumann and Römheld, 1999; Pearse et al., 2006). These species can exude massive amounts of malonate, malate, and citrate, which are some of the most efficient P-mobilizing carboxylates (Hinsinger, 2001). Thus, it is generally expected that legumes facilitate P acquisition of the intercropped cereal, although many legume species do not exude carboxylates at rates any greater than most cereals. Only one study (Li et al., 2010) focused on carboxylate composition and concentrations in the rhizosphere of intercropped species: maize (*Zea mays*) and white lupin or faba bean (*Vicia faba*). Intercropping affected carboxylate composition for maize but had no effect on carboxylate concentration, plant biomass, or P acquisition. The experiment was inconclusive, and additional work is needed to ascertain the significance of this process in intercropping systems.

Intercropping studies, which have investigated the potential role of P-mobilizing compounds, have mainly focused on phosphatase activity (Li et al., 2004; Inal et al., 2007; Wang et al., 2007a). Root-excreted phosphatases may enhance soil P availability through hydrolyzing organic P. Li et al. (2003a) reported increased P acquisition from organic sources (phytate) in wheat intercropped with chickpea compared with wheat grown with a solid barrier separating its roots from those of chickpea. They showed no such effect when the source of supplied P was inorganic ( $FePO_4$ ), which suggests that chickpea did facilitate P acquisition by the intercropped wheat as a consequence of its ability to hydrolyze the organic P supplied, presumably by phosphatase secretion. Li et al. (2004) observed both in hydroponics and soil-grown plants that higher phosphatase activity was observed for chickpea than for maize. Intercropping, however, did not affect the phosphatase activity of either species, although maize biomass and P acquisition were enhanced. The enhanced biomass and P acquisition of the cereal could not be related to increased phosphatase activity in intercropping compared with maize grown alone because it also occurred when only inorganic P was supplied. Wang et al. (2007a) conducted a similar experiment but with another soil, using different species and growth duration. No intercropping effect was observed when P was added in an organic form (phytate), but biomass, P acquisition, phosphatase activity, and P availability all increased when inorganic P was added. Relationships between rhizosphere processes such as phosphatase secretion and P facilitation have not been clearly established yet. It is important to note that a large proportion of phosphatase activity in the rhizosphere is not directly the consequence of the secretion of root-borne enzymes but rather derives from microbial activities (see below). None of the published

work on intercropping systems has attempted to determine the origin of the measured phosphatase activities, due to methodological limitations. To a lesser extent, this also applies to rhizosphere pH and organic ligand concentrations.

All of the above-mentioned rhizosphere processes occur over rather small spatial scales. While protons/hydroxyls can diffuse several millimeters away from root surface, carboxylates and most enzymes are expected to be strongly adsorbed onto soil particles and thus poorly mobile in the rhizosphere, rarely diffusing over distances greater than 1 mm millimeter or so (Hinsinger et al., 2009). Thus, in the absence of long root hairs or effective mycorrhizal symbiosis, root proximity is required for the occurrence of positive interactions that involve the release of P-mobilizing exudates. Thus, in contrast to spatial niche separation, intimate intermingling of roots of the two intercropped species is needed for P facilitation to occur. This is supported by root barrier experiments, either in the field or in pot culture (Fig. 4), which have consistently shown that better growth and/or P acquisition is achieved when there is no physical barrier between the roots of intercropped species. Using an elegant modeling approach, Raynaud et al. (2008) demonstrated that under conditions where the diffusion of citrate is spatially restricted, as would be expected to occur in most soils, only the few neighboring roots of the non-exuding species could benefit from the increased P availability due to citrate released by roots of the exuding species. This spatial restriction not only stems from the poor mobility of P-mobilizing compounds released by roots, such as protons/hydroxyls, but especially carboxylates or phosphatases. It is also necessary for the released phosphate ions to be able to diffuse back toward the roots of the facilitated species. The need for close proximity (within millimeters) between roots may be offset by long root hairs and more so mycorrhizal symbiosis, which can confer access to P resources farther away from roots of the facilitated, intercropped species. Besides spatial considerations, temporal variations of either uptake or release of P-mobilizing compounds should be accounted for, as the age of a root segment can considerably influence its physiology. This has been especially documented for the release of protons and carboxylates in cluster roots of white lupin (Neumann and Martinoia, 2002).

Besides the exudation of P-mobilizing compounds, other processes may also induce changes in rhizosphere P availability as a consequence of interactions with the uptake of other nutrients, as for example N uptake and its effect on rhizosphere pH. The potential role of calcium (Ca) uptake has been recently demonstrated by Devau et al. (2010). Increased P availability in the rhizosphere of durum wheat could not be explained fully by P uptake combined with rhizosphere alkalization due to nitrate nutrition. However, when accounting for Ca uptake, Devau et al. (2010) obtained a good agreement between measured and



**Figure 4.** Maize/faba bean intercropping performance in two field experiments with three barrier treatments: a solid, impermeable plastic sheet preventing root contact and solute transfers between the species (black bars); a nylon mesh that prevented root contact but enabled solute transfer (gray bars); and no barrier between the root systems (white bars). A, Grain yield of maize and faba bean from Li et al. (2007), reprinted with permission from the National Academy of Sciences of the United States. B and C, Grain yield (B) and P uptake (C) of maize and faba bean from Li et al. (1999, 2003b), reprinted with permission from Springer Science+Business Media. For each species, different letters indicate significant differences among barrier treatments ( $P < 0.05$ ).

modeled rhizosphere P availability. Ca interacted with P via its effect on surface charges especially for clay minerals at neutral pH, thereby promoting the adsorption of phosphate ions and decreasing P availability. The uptake of Ca by roots thus had the opposite effect of increasing P availability. Given that Ca uptake can substantially differ between species, with legumes generally taking up more Ca than cereals, legumes

may thereby facilitate P acquisition of the intercropped cereal.

Unfortunately, we have little experimental evidence to support the facilitation of P acquisition in intercropping. Causal relationships between increased P acquisition and rhizosphere processes altering P availability are often lacking, in contrast with the well-documented role of N facilitation in cereal/legume intercropping. Only a few studies have attempted to measure both rhizosphere processes and changes in P availability (Song et al., 2007; Wang et al., 2007a; Li et al., 2008) or P acquisition in intercropping systems. In addition, rhizosphere processes may vary greatly with soil type and plant species (Hinsinger, 2001; Hinsinger et al., 2009), and P availability in the rhizosphere of intercropped species has been mostly studied in alkaline/neutral soils. These complex interactions need to be examined in a range of soil types including acidic soils (Wang et al., 2007a, 2007b; Li et al., 2010). For instance, the hypothesis of facilitation of cereal P acquisition due to legume-mediated rhizosphere acidification has only been tested in alkaline/neutral soils (Li et al., 2003a, 2008; Cu et al., 2005). It should also be tested in acidic soils, where alkalization might prove more efficient at increasing P availability.

#### MICROBIALLY MEDIATED RHIZOSPHERE INTERACTIONS

Besides direct root-induced chemical processes in the rhizosphere, facilitation can also occur as a consequence of shifts in the microbial community structure, biomass, or activity (Fig. 3). Plant species exert a selective influence on rhizosphere microbial communities due to differences in amounts and composition of root exudates and rhizodeposits (Hartmann et al., 2009; Dennis et al., 2010). For instance, differences in fungal community structure in the rhizosphere of white lupin were attributed to citric acid, while differences in bacterial community structure were attributed to the presence of cis-aconitic, citric, and malic acids (Marschner et al., 2002). In addition, roots exude a range of secondary metabolites and signaling molecules that shape microbial communities and are implicated in root-root and root-microbe communication (Walker et al., 2003). Rhizosphere communities can thus vary with plant species (Marschner et al., 2001, 2006; Smalla et al., 2001) and/or plant genotype-soil interactions (Marschner et al., 2001, 2004). In addition to the selective effect of rhizodeposition, there is increasing evidence that soil chemical properties such as pH have a major influence on the structure of soil microbial communities (Philippot et al., 2009; Rousk et al., 2010). To what extent this would apply to rhizosphere pH changes remains an open question (Hinsinger et al., 2009), which would be worth testing in cereal/legume intercropping systems.

Several studies have shown significant changes in microbial community structure in the rhizosphere of

intercropped species compared with those of sole crops (Song et al., 2007; Wang et al., 2007a; Li et al., 2010). Intermingling of roots of the intercropped species can result in a common microbial community structure, which might simply be a mixture of the respective communities of each of the two species (Wang et al., 2007a). However, in the rhizosphere of intermingled roots, a greater diversity of organic compounds could be expected if there are differences in root exudate composition between the intercropped species. In that case, the microbial community of intercropped species would not be a simple mixture of the communities of each of the two species. So far, effects of intercropping on microbial community structure are contradictory. Fan et al. (2011) found little effect of maize/faba bean intercropping on the community structure of ammonia oxidizers. The sampling technique and growth stage may also explain discrepancies among studies.

Changes in microbial community structures alone are not as important as changes in microbial biomass and activity, which can influence plant growth by altering root growth via hormone production or nutrient availability through mineralization (Song et al., 2007; Richardson et al., 2009; Fan et al., 2011). Marschner et al. (2006) observed a correlation between microbial P and acid phosphatase activity under P-limiting conditions. However, there is often a weak link between microbial community composition and activity, because many of these functions are carried out by a wide range of microorganisms, which form substrate guilds (Zak et al., 1994). The consequence of such functional redundancy is that changes in the abundance of a single species often have little effect on a given function (Miethling et al., 2003). However, even for functional communities with low levels of redundancy, like nitrifiers (ammonia-oxidizing archaea and bacteria), their community structure was not modified by intercropping (Fan et al., 2011). Nevertheless, there are indications that changes in overall microbial community composition can be correlated with changes in certain microbial activities, including phosphatase activities (Kandeler et al., 2002).

In order to assess the effect of microbial community structure on P acquisition of intercropped species, specific functional groups of microorganisms should be targeted, such as those implicated in the mobilization of inorganic or organic P pools in soils. The capacity to increase the availability of inorganic P is widespread across soil microorganisms, as it originates in the production of protons, organic acids, and ligands, which are ubiquitous physiological traits among rhizosphere P-solubilizer microorganisms (Richardson et al., 2009). Besides P-solubilizer microorganisms, numerous microorganisms also use phytate, an important pool of soil organic P (Turner et al., 2002), presumably through the production of phytases (Jorquera et al., 2008). These authors found that the proportion of phytase-mobilizing bacteria from the rhizosphere of graminaceous species (wheat, 19.6%; oat [*Avena sativa*], 17%) was twice that

found for a legume (yellow lupin [*Lupinus luteus*], 8.2%). Although their approach was based on culturable bacteria only, these results suggest that intercropping species such as cereals and legumes may select different functional bacterial populations, resulting in varying capacities to mobilize phytate in the rhizosphere. To confirm this hypothesis, it will be necessary to develop molecular tools to probe microbial phytase genes, whether from bacterial or fungal origin. Unfortunately, phytases belong to four classes (Mullaney and Ullah, 2007), and molecular tools have been designed so far only for one class, the  $\beta$ -propeller phytases (Jorquera et al., 2011), corresponding to alkaline phytases found only in bacteria (Lim et al., 2007).

Another potential indirect effect in the rhizospheres of intercropped species is enhanced nutrient mineralization due to the priming effect. The priming effect is defined as the change in soil organic matter (SOM) decomposition rates, resulting from the addition of fresh organic matter (Blagodatskaya and Kuzyakov, 2008). Thus, it can occur in the rhizosphere via root turnover and rhizodeposition (Cheng, 2009). Fontaine et al. (2011) suggested that microorganisms use the energy from this fresh material to decompose SOM in order to release organic N when inorganic N is limiting. P limitation has never been proven to provoke a priming effect, but it may be likely in ecosystems that are primarily P limited, such as in the tropics. A positive priming effect (stimulation of SOM mineralization) should lead to the recycling of organic N and P and may ultimately enhance plant growth (Kuzyakov et al., 2000). Decomposition of the recalcitrant SOM is not accessible to all microorganisms and is in fact restricted to populations endowed with special enzymatic capacities. All those microorganisms have not yet been clearly identified, but a few phylogenetic groups are suspected to share this function (Bernard et al., 2007; Fontaine et al., 2011). As a consequence, the priming effect is dependent on both the microbial community composition and the quality of the fresh organic substrate. Actually, highly labile substrates would be used rapidly by populations that allocate their energy to growth rather than enzymatic machinery. Polymerized or aromatic compounds are more prone to generate some priming effect than Glc (Fontaine et al., 2011). The quantity and the quality of rhizodeposits may thus influence the structure and the diversity of the rhizosphere microbial community, and priming effect intensity should vary accordingly. Cheng (2009) indeed measured a 2-fold larger priming effect in the rhizosphere of pea (*Pisum sativum*) than in that of wheat. The priming effect has never been measured in the context of cereal/legume intercropping, but theoretically, rhizodeposits of one of the intercropped species that might release P in SOM could benefit the growth of the associated plant species via their intermingled rhizospheres.

The existence of interconnected, common mycorrhizal networks (CMN) bridging the roots of two plants

may also increase P availability to intercropped species. Direct transfer of nutrients between the intercropped species via CMN has been documented for N but not yet for P. Using  $^{15}\text{N}$  tracer, Li et al. (2009) showed that there was little transfer of N to the intercropped species when the donor was the cereal (rice [*Oryza sativa*]), with no significant role of CMN. In contrast, the transfer of N was much increased by the development of CMN when the donor species was the legume (mung bean [*Vigna radiata*]), which contributed up to 16% of the N taken up by rice.

## CONCLUSION

Current evidence for improved growth and nutrition in cereal/legume intercropping systems holds great promise for ecological intensification of agroecosystems. Much of our knowledge of nutrient efficiency in such systems has concerned N, especially with regard to legume  $\text{N}_2$  fixation. Studies on P are rare, and few of these distinguish between complementarity and facilitation or provide convincing evidence that a specific rhizosphere process explains the improved P efficiency when cereals and legumes are intercropped. Additional research is needed to confirm whether positive interactions occur in intercropped cereals and legumes, which could be manipulated to improve P acquisition efficiency for both low input and intensive agroecosystems (Zhang et al., 2010). Experiments need to be specifically designed for such purposes. Given the complexity of the underlying mechanisms, mechanistic modeling should also be further developed and tested.

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