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Intercropping with legume for agroecological cropping systems: complementarity and facilitation processes and the importance of soil microorganisms. A review

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Highlights

- Intercropping systems promote complementarity between plants, legumes in particular and facilitation processes in soil
- Complementarity/facilitation processes lead to better exploitation of soil resources
- Plant production is positively correlated with soil microbial abundance and diversity
- Increased attention should be paid to innovative perennial systems with intercropping for facilitative root interactions

Abstract

Intercropping is a powerful way to promote a more diversified plant community in the field, thereby enabling complementary and facilitative relationships. In these systems, legumes are a key functional group, and are highly valued for the agroecological services they provide. This review identifies the different complementarity and facilitation processes in soils in intercropped legume/cereal systems and the key role of soil microorganisms in these processes.

The intercropped legumes/cereal systems reduce inter-specific competition by enhancing complementarity/facilitation processes thereby improving the exploitation of resources, which is, in turn, reflected in the increase in plant production corresponding to greater efficiency of the agroecosystem as a whole.

Plant production, including above- and belowground biomass, is positively correlated with microbial abundance and diversity. This microbial life is assumed to play a significant role in the availability and transfer of soil nutrients to plants as well as in plant health and soil fertility. Although we are currently unable to identify a reliable and exhaustive pattern of plant-microbe interactions, perhaps simply because no universal relationship exists between plants and microorganisms, reliable scenarios reveal strong trends and define the conditions required for successful intercropping systems and microbial interactions.

Given our incomplete knowledge of facilitation processes and belowground interactions, intercropping systems must learn from and apply the experience gained in successful experiments. Intercropping dynamics play a critical role in explaining the establishment of facilitative root interactions and finally suggest perennial plant associations may be more effective than annual ones.

Keywords: intercropping; rhizosphere; legumes; soil microorganisms; facilitation; complementarity.

Introduction

Modern agriculture, which produces high yields through the generous use of chemical inputs and non-renewable energy, is currently being called into question. The recent past has revealed how costly this model can be in terms of public health and environmental integrity (Altieri, 2000; Tilman et al., 2002). The latest research underlines the importance of designing cropping systems using ecological principles and ecosystem services to enhance agroecosystem sustainability and production efficiency, offloading chemical inputs and non-renewable energy (Clergue et al., 2005; Moonen and Bàrberi, 2008; Wezel et al., 2014). This approach is known as 'agroecology' (Gliessman, 1990; Wezel et al., 2014).

Following agroecological guidelines, a wide range of practices has been developed to improve the ecological functioning of cropping systems including intercropping, crop rotations, cover cropping, green manure, reduced tillage, and agroforestry (Wezel et al., 2014). Intercropping, i.e. growing two or more crops together on the same land at the same time (Willey, 1990), has great potential, and is expected to substantially optimize cropping systems thanks to diversification.

So far, a large body of literature has investigated the widespread practice of cereal/legume intercropping. Based on the observation that, in natural ecosystems, legumes are normally found among grasses, many authors have considered legumes as a key species in promoting ecosystem efficiency (Altieri, 1999; Anil et al., 1998; Malézieux et al., 2009; Vandermeer, 1995; Vandermeer et al., 1998). Their use in intercropping system is largely explained by their nitrogen (N) fixing capacity, which makes them very valuable as green manure, especially in cropping systems with chronic nitrogen deficiency, i.e. organic farming (Bedoussac et al., 2015; Hauggaard-Nielsen et al., 2008). Intercropped legumes have proved to be capable of providing a wide range of additional services (Table 1) and of producing substantially higher yields than a sole crop—expressed as a land equivalent ratio (LER) higher than 1 (Willey, 1979).

Table 1. Agroecological services provided by cereal/legume intercropping systems

SERVICES		EVIDENCE FOR	REFERENCES
Provisioning	Yields	<ul style="list-style-type: none"> - Higher intercropping yields than for sole crop in low-input systems (<i>LER up to 2,2</i>) - Maintained or increased yield and quality through increased grain protein content (<i>up to 1% increase</i>) 	(Bedoussac and Justes, 2010a; Bergkvist et al., 2011; Hauggaard-Nielsen et al., 2008; Jensen et al., 2006; Willey, 1979) (Bedoussac et al., 2011; Hauggaard-Nielsen et al., 2008; Justes et al., 2009; Pelzer et al., 2012)
	Nitrogen dynamics	<ul style="list-style-type: none"> - Limited interspecific competition for N acquisition - Soil N enrichment - Increased N accumulation in plants - High N restitution through residues 	(Amossé et al., 2014, 2014; Corre-Hellou, 2005; Corre-Hellou et al., 2006; Fustec et al., 2010; Hauggaard-Nielsen et al., 2009; Shili-Touzi et al., 2010; Singh et al., 1986; Stern, 1993; Wichern et al., 2008)
	Use of resources	<ul style="list-style-type: none"> - Better overall exploration of resources - Improved resource use efficiency (<i>light, nitrogen, water use efficiency improved up to 20%</i>) 	(Bedoussac and Justes, 2010b; Brooker et al., 2015; Matusso et al., 2014; Midmore, 1993; Morris and Garrity, 1993; Vandermeer et al., 1998a; Willey, 1990)
Regulation & Maintenance	Weeds	<ul style="list-style-type: none"> - Improved weed control 	(Amossé et al., 2013a; Haramoto and Gallandt, 2004; Kruidhof et al., 2008; Liebman and Dyck, 1993; Valantin-Morison et al., 2014)
	Pests	<ul style="list-style-type: none"> - Reduced attacks and damage caused by pests (<i>up to 50% of pest species reduced</i>) 	(Ratnadass et al., 2012; Risch, 1983; Smith and McSorley, 2000; Trenbath, 1993)
	Soil	<ul style="list-style-type: none"> - Increased soil stability and C content - Better soil infiltration - Improved chemical composition - Enhanced nutrient turnover and mineralization - Increased soil biology and diversity 	(Brussaard, 1997; Brussaard et al., 2007; Carof et al., 2007; Dabney et al., 2001; Gregorich et al., 2001; Karlen et al., 1997; Latif et al., 1992; Oelbermann and Echarte, 2011; Qiang et al., 2004; Whipps, 1990)

Recent studies have demonstrated the particular importance of facilitative plant root interactions in mitigating stressful conditions and increasing yields. New insights into facilitation processes in particular emphasize the importance of intercropped roots in mobilizing limited or unavailable nutrients such as phosphorus in harsh environmental conditions (Betencourt, 2012; Hauggaard-Nielsen and Jensen, 2005; Latati et al., 2014, 2016; Li et al., 2014) and suggest a key role for soil organism diversity in the rhizosphere in these processes (Hinsinger et al., 2011b; Tang et al., 2014).

However, belowground interactions between intercropped roots and soil organisms are still largely unexplored and a very few data are available on facilitation processes (Brussaard et al., 2007). The involvement and role of the diversity of soil organisms is an open question, especially when we consider the importance of soil microorganisms. The abundance, role and function of microbial communities are poorly accounted for in plant facilitation and appear to be the missing link in understanding plant growth, nutrition and their interactions with the plant's immediate environment (Lemanceau et al., 2014; Philippot et al., 2013). Intercropping favors the development of different types of roots and changes overall root distribution and architecture, as well as exudation processes in the rhizosphere (Bargaz et al., 2015a; Hauggaard-Nielsen and Jensen, 2005; Hinsinger et al., 2009; Li et al., 2014). Consequently, intercropping will influence both the extent and nature of the relationships between plants and microorganisms, thereby enabling new beneficial interactions.

The aim of this review is to underline the valuable role played by cereal/legume intercropping not only in improving crop yields but also in agroecosystem sustainability by exploiting the plant complementarity concept for the acquisition of soil resources and for the facilitation of processes that occur in the rhizosphere thanks to positive plant-soil-microorganism interactions.

First, we consider complementarity in intercropping systems and underline the co-occurrence of both complementary and competitive relationships. We then discuss why the facilitation concept is required to understand the positive interactions within the plant rhizosphere. In so doing, we confirm and underline the distinction made by Justes et al. (2014) between complementarity and facilitation, although in practice such a distinction is hard to make (Loreau and Hector, 2001). Complementarity refers to partitioning resources, reducing competition between species, while facilitation enables positive interactions between plant species responsible for supplementary services. For instance, facilitation occurs when one species is able to mobilize an initially unavailable pool in the soil thanks to the presence and action of another species. Formerly underestimated, the notion of facilitation is now widely recognized and substantial research has been conducted on positive interactions (Betencourt, 2012; Brooker et al., 2008; Doelsch et al., n.d.; Stachowicz, 2001).

Second, we discuss the role of microorganisms in facilitation and how intercropping can favor microbial abundance and activity. The second section is based on the many studies that demonstrate the role of bacteria (Ahmad, 2008; Compant et al., 2010; Vacheron et al., 2013) and mycorrhizae (Gianinazzi et al., 2010; Jeffries et al., 2003; Johansson et al., 2004) in plant interactions, health and nutrition in the rhizosphere.

Third, we discuss the management of intercropped systems by farmers and their need to reach compromises and find the best trade-offs to ensure they achieve their production goals and the ecological potential of the system they select.

The overall aim of the review is to promote cereal/legume intercropping for sustainable agriculture, but we include a thorough discussion of soil microbial issue, considered as a key point in plant relationships and resources use.

1. Complementarity and facilitation interactions

1.1. What is complementarity?

The most intricate documented mechanisms that improve crop performance concern the better use of resources by intercropped species (Bedoussac, 2009; Bedoussac et al., 2015). Known as "interspecific complementarity", this concept suggests that crops differ in the way they find and use resources, thereby limiting interspecific competition. Complementarity can be categorized as *temporal*, *spatial* or *chemical* partitioning (Justes et al., 2014). Plant species can be complementary when there is a significant time lag between their needs. Experiments in relay-intercropping provide examples of how to take advantage of delays in growth and development. When clover is sown in the spring under a winter wheat cash crop (Amossé et al., 2013b), the growth of the main crop is not impaired by the growth of the legume, which remains poorly developed during the intercropping period and then increases its growth rate once the wheat has been harvested. *Spatial* complementarity means that the nutrient uptake process occurs in different locations depending on rhizosphere interactions and on the traits of the intercropped plants concerned. *Spatial* complementarity mostly depends on root architecture and rooting depth, which determine the water or nutrient extraction depth (Hauggaard-Nielsen and Jensen, 2005). Because of the depth-dependent extraction capacity, *spatial* complementarity can also be defined as vertical niche stratification. Studies conducted in pea-barley intercrops (Hauggaard-Nielsen et al., 2001a) provided evidence for such spatial distribution by showing that barley root systems use deeper soil layers when intercropped with pea. The spatial segregation of different root systems is also frequently reported in agroforestry where plants exploit root plasticity to avoid excessive root competition and to explore different regions of the soil (Schroth, 1998). *Chemical* complementarity refers to the ability of species to mobilize different chemical forms of nutrients. Much less common, *chemical* complementarity most frequently refers to the ability of legumes to fix nitrogen from the atmosphere, which other species cannot do.

But, despite the different types of complementarity, most field experiments show a combined effect of *temporal*, *spatial* and *chemical* complementarity rather than a single form of partitioning and sharing resources. In the case of durum wheat intercropped with winter pea (Bedoussac and Justes, 2010a), complementary plant growth and N acquisition dynamics were observed as well as better use of light thanks to aerial spatial complementarity. To unravel the intricacies in the pattern of complementarity between plants, the global efficiency of different cereal/legume intercropping models can be inferred from global productivity per unit area using the LER indicator (Land Equivalent Ratio). Several intercropping plant models have been tested in this way. For instance, a wheat/chickpea model showed a LER value of around 1.5 (Banik et al., 2006). Land use efficiency and productivity largely depends on the complementary processes underlying the choice of intercropping model. Complementarity mechanisms need to be seen as the consequence of adaptive plant traits, including root plasticity or nitrogen fixation (Bargaz et al., 2015a; Jensen, 1996), expressed in stressful situations (limited resources availability or significant competition with another species; Bedoussac et al., 2015; Fridley, 2002) rather than as the result of permanent and systematic plant "behavior".

1.2. Complementarity in nutrient acquisition

1.2.1. Complementarity in nitrogen acquisition

Adding legumes in crop fields is justified by their natural ability to exploit atmospheric nitrogen (N_2). This additional source of N is expected to (i) avoid interspecific competition between crops and legumes for N acquisition (Carof, 2006; Hauggaard-Nielsen et al., 2008), (ii) and to make substantial N contents available for the following crop through increased soil N content after destruction of the legume cover crop. Amossé et al. 2014 found that intercropped legumes could store between 40 and 100 kg N/ha in the aboveground parts of plants. Up to a 30% increase in the yield of the following maize crop has been shown to be positively correlated with the development of legumes and N accumulation in legume tissues (Amossé et al., 2014; Bergkvist et al., 2011).

The ability of legumes to fix atmospheric nitrogen is the result of their symbiosis with a *Rhizobium* bacteria, located in specific root structures called nodules. This type of symbiosis has been widely studied but experiments have shown that the formation and activity of the nodules can vary. Jensen (1996) demonstrated that N_2 fixation by pea at plant maturity was $17,7\text{g N m}^{-2}$ when pea was grown as intercropped species with barley whereas it was only $5,1\text{ g N m}^{-2}$ when pea was grown alone. Legumes preferentially absorb nitrogen in inorganic form and fix atmospheric nitrogen only when soil N is limiting due to low availability or increased N-competition due to intercropping. This trait makes legumes highly desirable since they can substitute one source of N for another when necessary. Studies by Hauggaard-Nielsen et al. (2008) comparing *nitrogen derived from the atmosphere* (Ndfa) in legumes growing either in a pure stand or associated with another crop, clearly confirmed this adaptive trait which is aimed at using a minimum of energy for a maximum of benefits. The rate of N_2 fixation of legumes is therefore negatively correlated with the inorganic N content in the soil (Mahieu, 2009). Thus, the growth and activity of nodules under intercropping are enhanced by regulation of N-feedback (Parsons et al., 1993). Even if the regulation of N_2 fixation involves other parameters like P availability or soil pH (Schulze, 2004; Vance et al., 2000; Zhang and Li, 2003), this straightforward feedback mechanism is commonly considered to explain the valuable use of additional nitrogen pool from legumes as an effect of the complementarity mechanism.

1.2.2. Complementarity in phosphorus acquisition

After nitrogen, phosphorus (P) is the most limiting factor for plant growth (Vance et al., 2000). In fact, P is abundant in the soil but mainly in insoluble forms that are poorly available for uptake (Schachtman et al., 1998). This is especially critical in low-input systems since their supply of inorganic P is limited. In this context, cereal/legume intercropping systems been reported to enhance P acquisition (Cu et al., 2005; Hinsinger et al., 2011a). Regarding complementarity, Hinsinger et al. (2011a) explained that the geometry and volume of the rhizosphere largely determines the amount of P accessible to plants. Thus, the increase in root surface area under intercropping systems directly improves soil exploration. Moreover, plants have been shown to be capable of receiving environmental stimuli and modifying their root distribution depending on nutrient availability and competition with the root systems of other species (Cahill et al., 2010). Such plant behavior confirms that adaptive foraging strategies are real and fully involved in the efficiency of soil exploration. Although this process and "root decisions" (Hodge, 2009) are far from thoroughly understood, this reality confirms the occurrence of *spatial* complementarity in intercropping systems in which plants can use a restricted foraging strategy and target zones with specific nutrients.

Finally, cereal/legume intercropping has revealed its capacity to improve P-uptake efficiency by depleting specific inorganic pools. Without mentioning any nutrient transfer or better P availability through the action of one species, Cu et al. (2005) showed that white lupine and

wheat preferentially use either citric acid leachable P or a water leachable soil P pool, thereby supporting the hypothesis of Turner (2008) concerning resource partitioning for soil phosphorus. However, like with other cereal-legume intercropping models (Li et al., 2007, 2003), these findings suggest that this strict complementarity is hard to dissociate from other changes in the rhizosphere induced by intercropping, like soil pH or changes in enzymatic activity involved in the solubilization of inorganic P. But even if the boundaries of complementarity are not clear, it is likely that a general partitioning process makes it possible to shorten the length of the period of competitive relationships between plants (Vance, 2001).

1.3. Complementarity in the field, where theory meets practice:

Introducing intercropping practices in modern agriculture can be difficult. Complementarity is based on a delicate balance but can rapidly turn into competitive relationships. In fact, competition almost always occurs within plants communities (Vandermeer, 1992). Callaway and Walker (1997) talk about the "co-occurrence" of negative and positive interactions. The challenge is thus to ensure sufficient complementarity to compensate for - or overcome - interspecific competition. In the case of intercropped durum wheat and winter pea (Bedoussac and Justes, 2010a), yields were increased by about 20% compared to the yields of wheat grown as sole crop. This increase was shown to be the result of the better use of light (+10%), alternative growth period, and enhanced N uptake thanks to the nitrogen fixing ability of the legume (Bedoussac and Justes, 2010b). However, this success has been shown to depend on the availability of soil nitrogen. When nitrogen fertilizers are applied, winter wheat becomes more competitive than the legume, thereby enhancing wheat growth to the detriment of the legume. The same results have been obtained by other authors (Corre-Hellou et al., 2006; Jensen, 1996), highlighting better competitive traits in barley for soil N due to the growth dynamics of both roots and aboveground plant parts and the nitrogen supply. In the case of high soil mineral nitrogen availability, such observations underline the shifting balance between complementarity and competition and the importance of initial resource availability (Fridley, 2002). The balance between competition and complementarity changes constantly, depending on changes in environmental conditions or on the stage of plant development. For instance, as nodules are not well developed in the early stages of the life of a legume (Voisin et al., 2002), until the legume acquires sufficient ability to fix atmospheric nitrogen, the crop and the legume are in direct competition for mineral nitrogen.

In the case of incident light, it is even clearer that competition is unavoidable. When the whole combined canopy is measured, the total leaf area index (LAI) is substantially higher than when one species is measured (Willey, 1990). But one species is usually dominant, i.e. its growth is not limited by light, whereas the other species is growth limited, since it fails to obtain sufficient solar radiation (Bedoussac, 2009; Carof, 2006; Corre-Hellou, 2005). This dominant/subordinate relationship is thought to be determined by the LAI, aerial architecture, height, and growth dynamics (Midmore, 1993). However, the lack of captured light can be partly offset by a better conversion efficiency ratio (Willey, 1990).

The same kind of reasoning applies to water resources. Intercropping can be profitable when it exploits a large volume of soil and uses a higher soil water profile. However, this advantage is based on the suitability of the traits of the species cultivated— water requirements, root architecture – and the soil water content (Natarajan and Willey, 1986; Semere and Froud-Williams, 2001; Zegada-Lizarazu et al., 2006). Indeed, in water-limiting conditions, the most competitive species will play a dominant role while the growth of the less competitive species will be affected. In that sense, Zegada-Lizarazu et al., (2006) demonstrated unchanged growth of cowpea under drought conditions while the intercropped pearl millet lost biomass.

To sum up, growing several plant species together naturally involves competitive interactions – either for nutrients, light or water. But such interactions are not necessarily a handicap as long as complementarity is stronger than competition and improves the overall use of resources (Bedoussac et al., 2015). Using complementarity as an approach means considering the whole canopy and the overall production efficiency to determine the advantage of intercropping despite unavoidable background competition.

1.4. Where does the complementarity approach fail? The relevance of the facilitation concept

Concerning resource partitioning, a complementarity approach does not explain the positive interactions observed in the field. Especially concerning belowground interactions, many studies have shown that cereal/legume systems can promote beneficial interactions in which plants benefit from additional services that partially overcome competition and improve their growth or quality. Jensen and al., (2006), and Bedoussac (2009), showed that wheat or barley intercropped with legumes resulted in an increase in grain protein content (GPC); Hinsinger et al. (2011a) and Latati et al. (2014) showed that P availability increases under intercropping; Singh et al. (1986) and Tang et al. (2014) reported improved microbial activity or biomass when legumes are used as intercrops; Li et al. (2007) showed that legumes can acidify the soil rhizosphere thereby increasing the release of nutrients into the soil solution; Latati et al. (2016) reported that enhanced P availability under intercropping improves the efficiency of the rhizobial symbiosis (EURS) with the legume and the N nutrition index (NNI) for the intercropped cereal (maize). All these examples are evidence that managing plant diversity has consequences for soil environmental conditions and can enhance interactions within plant communities (Fridley, 2001). When beneficial, these interactions demonstrate the importance of facilitation processes in the agroecosystem, which enable the creation of new pools of resources and promote their use (Callaway, 1995).

Generally speaking, the capacity of plants to acquire provisioning resources under intercropping depends on the result of both complementarity plant facilitation processes, all occurring in the field but at varying levels. Complementarity is mainly responsible for limiting competitive interactions by improving resources partitioning, while facilitation provides additional services by improving environmental growth conditions and resources availability. Even if facilitation has been shown to be involved in plant communities, quantifying its effect on intercropped systems is still a major challenge. This difficulty explains why agricultural models that attempt to incorporate the notion of facilitation in field management are still rare. Indeed, a wide range of factors influence the occurrence of effective positive interactions between plants, including the plant species (Semere and Froud-Williams, 2001), stress conditions (Callaway et al., 2002; Maestre et al., 2009), soil conditions (Degens et al., 2000; Zegada-Lizarazu et al., 2006) and the use of fertilizers and pesticides. Nevertheless, previous studies confirm the relevance of considering the facilitation process in low-input systems (Brooker et al., 2008; Fridley, 2001; Stachowicz, 2001; Zak et al., 2003). In order to better understand the mechanisms involved in rhizosphere interactions that create better growth conditions, we suggest classifying the facilitation processes according to the degree of "directness" of the interaction. *Indirect* facilitation refers to beneficial physical, chemical or biological changes that occur in the rhizosphere (changes in environmental conditions) that enhance nutrient availability and plant uptake. *Direct* facilitation, much less frequently recognized and reported in the literature, refers to the improvement in plant nutrition through the transfer of nutrients from one plant to another, in which the rhizosphere is the interface.

1.4.1. Direct facilitation

Rhizodeposition is the release of organic and inorganic compounds from living roots. This includes specific compounds like root border cells or sloughed root cells, release of root hair cells, and the release of non-specific compounds from the roots like exudates, mucilage, enzymes, ions, or secretions (Nguyen, 2003; Wichern et al., 2008). Rhizodeposition is the process by which legumes enrich the soil N-pool by providing significant amounts of nitrogen – known as *Nitrogen derived from Rhizodeposition* (NdfR; Fustec et al., 2010; Mahieu et al., 2014). Much of this rhizodeposition is determined by the total N-assimilation of legumes, total root production and the age of the plant – NdfR increases at maturity because senescing roots release N into the soil (Wichern et al., 2008). Reviewing laboratory studies, Wichern et al. (2008) reported that rhizodeposits account for from 15% to 96% of the belowground plant biomass, with a median of 73% in legumes but only 57% in cereals. Jensen (1996) experimented N-transfer from field pea to spring barley and showed an increasing amount of pea-derived N in barley over time (up to 19% of barley N). These findings are in agreement with those of Walker et al. (2003), who explained that, during plant growth, N is deposited in the rhizosphere as a result of the continuous turnover of roots and nodules. Unfortunately, many other studies failed in their attempt to reveal significant N-transfer in the field (Giller et al., 1991; Hauggaard-Nielsen et al., 2001b), suggesting either inadequate ¹⁵N-labelling techniques in field experiments or marked variability of such nutrient transfers. However, Wichern et al. (2008) estimated that pea plants could release about 129 kg N/ha during their growth cycle, including 56 kg from rhizodeposition. In contrast, wheat was estimated to release only 26 kgN/ha as rhizodeposits.

As far as we know, there are no similar data on potential P transfer from rhizodeposition. However, in addition to the above-mentioned studies on improved root exploration and distribution promoting P uptakes (Hinsinger et al., 2011a), evidence for increased P mobility in the soil and within the rhizosphere have been reported under intercropping (Zhou et al., 2006) and suggest mutual benefits for both species through better P migration and transfer between roots. Moreover, P and N-facilitation may be possible from a *temporal* point of view. A significant delay in plant growth, ensured by different sowing dates for instance, can improve nutrient availability when mineralization of some plant residues begins while the intercropped plants are still growing and provide substantial amounts of resources directly in their rhizosphere (Hinsinger et al., 2011a).

1.4.2. Indirect facilitation (changes in the environmental conditions in the rhizosphere)

Facilitation also occurs when intercropping modifies the crop environment. Indeed, improved growth conditions and better access to soil resources may result from these environmental changes. In that sense, Callaway (1995) includes among facilitation mechanisms changes in light and temperature, soil moisture, the concentration of nutrients in the soil solution, improved oxygenation, changes in the substrate, or the introduction of other beneficial organisms. For example, intercropping has been shown to be very useful for weed and pest management (Amossé et al., 2013a; Corre-Hellou et al., 2011; Trenbath, 1993; Valantin-Morison et al., 2014; Vandermeer, 1992), which can be considered as *indirect* facilitation since it reduces competition with weeds for resources and enables disease alleviation. However, in this review, we focus on changes in the rhizosphere.

Increased belowground biomass and root activity have a major impact on soil properties and on the soil solution. In maize/legume intercropping experiments, increased root activity has been shown to have positive effects on soil aggregation and to significantly decrease dry bulk density and soil resistance to root penetration (Latif et al., 1992). Studies conducted by Carof (2006) revealed the role of a living cover crop root in maintaining soil structure and hydraulic

conductivity over time. This author suggested that it can even provide long-term benefits. Even if explicit data on soil water content in cereal/legume intercropping is extremely rare, studies conducted by Celette et al. (2008) on intercropped vineyards showed that the soil water profile could be improved by reduced run-off and enhanced soil infiltration. The same results are assumed under cereal/legume intercropping.

This intensified root activity, and consequently the increase in rhizodeposits, improves soil carbon content and has a positive impact on nutrient storage and on the soil exchange capacity (Balesdent et al., 2011; Farrar et al., 2003; Oelbermann and Echarte, 2011).

In addition to the release of nutrients and carbon by rhizodeposition, there is evidence that a mixture of exudates (organic acids, enzymes, vitamins, amino acids, phytosiderophores, etc.) released by legumes can play a major role in modifying the chemical composition of the rhizosphere and transforming unavailable P, Ca, and Fe resources into available resources through solubilization or chelation of Fe (Dakora and Phillips, 2002; Fridley, 2002; Hinsinger et al., 2003). Studies on cereal/legume intercropping assume that the main process affecting N and P facilitation is the change in root-induced pH through fixation of N₂ by the legume (Bargaz et al., 2015b; Betencourt, 2012; Hinsinger, 2001; Hinsinger et al., 2003; Latati et al., 2014). Indeed, root exudation of protons, organic acids, carboxylates and phosphatases is favored and associated with atmospheric nitrogen fixation, thereby causing acidification of the legume rhizosphere. The acidification of the rhizosphere due to legume activity will likely benefit the intercropped cereal by increasing P availability through the dissolution of P minerals (Hinsinger et al., 2011b; Lambers et al., 2006; Vance et al., 2003). Intercropped pigeon pea, for instance, releases organic acids into the soil which solubilize significant amounts of phosphate from the iron-phosphate complex (Otani et al., 1996). The same process has also been studied in other legumes such as white lupine, faba bean or chickpea (Cu et al., 2005; Li et al., 2009, 2004; Marschner et al., 1986). Li et al. (2003, 2004, 2009) demonstrated that intercropping significantly facilitated indirect P uptake. Total P-uptake by plants increased by 68% when wheat/chickpea roots were intermingled rather than separated. In the same way, P supplied by phytate increased 1 to 5 fold when intercropped with chickpea, proving that chickpea roots facilitate P uptake. The concentration of carboxylates in the rhizosphere has also been shown to be influenced by the presence of the legume species in maize/faba bean intercropping (Li et al., 2009).

These indirect facilitation processes are particularly pronounced in alkaline/neutral soils, where P availability is even lower. Indeed, in alkaline soils, different authors described a dynamic feedback loop between the plant and the soil whereby exudation of protons and organic acids is influenced and stimulated by soil P deficiency and plant N nutrition (Bargaz et al., 2015b; Betencourt, 2012; Hinsinger et al., 2003; Neumann and Römheld, 1999; Tang et al., 2004). These aspects of plant/soil interactions are extremely interesting in the context of intercropping, since they suggest that competition for one resource (inorganic N), by enhancing symbiotic fixation of nitrogen (FSN), may stimulate facilitation of another resource like acid-soluble P (Hinsinger et al., 2011a). Moreover, the benefits of intercropping for plant N nutrition can also be highlighted since improved P availability has been shown to be associated with an increase in EURS (Latati et al., 2014, 2016) as well as with better N status (NNI) of the intercropped cereal (Corre-Hellou et al., 2006; Latati et al., 2016). These findings confirm that initial environmental conditions may affect the facilitation process, whereby the use and increased rate of N₂ fixation under intercropping is largely responsible for stimulating root activities and rhizosphere interactions, thereby improving resources use.

Findings showing increased microbial biomass and microbial activity when a cereal and a legume are intercropped clearly revealed the involvement of microbial life in this stimulation of the rhizosphere (Latati et al., 2014; Qiang et al., 2004; Tang et al., 2014). We thus assume that intercropping plays a critical role in soil biological diversity and in selecting functional soil microbial communities that rely on carbon fluxes in the plant rhizosphere and on signal molecules promoting mutualistic relationships (Bartelt-Ryser et al., 2005; Philippot et al., 2013; Qiang et al., 2004; Zak et al., 2003). Facilitation models should thus take such considerations into account.

2. When facilitation involves microbial life

2.1. The rhizosphere: a hub of plant-microbe interactions that promotes beneficial relationships

The soil rhizosphere is characterized by close links with microbial communities. The term rhizosphere refers to the volume of soil in the immediate vicinity of the roots. It provides an ideal living environment for bacteria, fungi and innumerable other organisms. Rhizodeposition and exudation by crop roots are crucial since they provide large amounts of nutrients to microbial communities (Hinsinger et al., 2009; Wichern et al., 2007). In this context, root exudation plays a key role in ensuring plant-microorganism interactions (Bais et al., 2006; Bertin et al., 2003; Morgan et al., 2005) and significantly shapes the structure of the microbial communities (Berg and Smalla, 2009; Hamilton and Frank, 2001; Qiang et al., 2004; Wieland et al., 2001). Therefore, changes in plant communities could stimulate specific functional traits of soil microbial communities (Bartelt-Ryser et al., 2005; Fridley, 2001; Zak et al., 2003; Zhou et al., 2015).

Beyond passive diffusion mechanisms, recent studies have shed new light on these plant-microorganism relationships in which both the plant and the microorganisms play active roles in the outcome of the plant-microbe interaction (Zhou et al., 2015). Through complex molecular exchanges during the process of communication (Faure et al., 2009; Hirsch et al., 2003; Johansson et al., 2004), bacteria or arbuscular mycorrhiza (AM) have been shown to be capable of providing supplementary dietary nutrients (Gianinazzi et al., 2010; Jeffries et al., 2003; van Kessel et al., 1985) and phytohormones involved in plant growth and root architecture (Bashan and de-Bashan, 2010; Drogue, 2013). They can also alleviate biotic and abiotic plant stress factors (Vacheron et al., 2015) and protect plants against pathogens as well as stimulate plant resistance (Audenaert et al., 2002; Lemanceau, 1992). All these positive influences are known as *phytobeneficial activities* and are seen here as a microbial facilitation process. Considering the value of such mechanisms, we now investigate to what extent cereal/legume intercropping can promote beneficial soil communities capable of plant facilitation. The main advantages of intercropping a legume and a non-legume appear to be due to the stimulation of rhizosphere activities based on legume N-fixing action, the associated exudates and the resulting changes in pH. We now investigate specific changes in microbial life caused by an intercropped legume.

2.2. Impact of intercropped legumes on beneficial soil-borne bacteria

In their studies, Alvey et al. (2003), found that legume crop rotations had a significant effect on the structure of the microbial communities and increased microbial diversity. Similar results have been obtained in intercropping experiments in which bacterial biomass and activity differed from those in mono-cropping systems (Latati et al., 2014; Li et al., 2009; Qiang et al., 2004; Song et al., 2006; Tang et al., 2014; Wang et al., 2007). Although more experiments are needed to identify the processes involved and the soil communities specifically targeted, the production and exudation of lectins by legumes has been shown to be capable of impacting *Plant Growth-*

Promoting Rhizobacteria (PGPR) mobility, improving root colonization and the phytobeneficial activity of these PGPR (Schelud'ko et al., 2009). In the same way, the secretion of certain flavonoids, naringenin, for example, involved in the well-known symbiotic association between legumes and *Rhizobium* bacteria, could be responsible for *Azospirillum brasilense* Sp245 (PGPR) lateral root colonization (Jain and Gupta, 2003). Likewise, the secretion of isoflavones by soybean roots attracts the beneficial bacterium *Bradyrhizobium japonicum* (Morris et al., 1998). Another example is the production of molecules that mimic N-acyl homoserine lactone (N-AHL), usually involved in a bacterial regulation process called quorum sensing (Teplitski et al., 2000). N-AHL has been found in several legume root exudates, where it influences the expression of specific genes that control quorum-sensing and bacterial coordinated activity. Confirmation that the composition of rhizosphere communities is species-specific (Marschner et al., 2001) also strongly support the hypothesis that intercropping creates favorable conditions for belowground interactions. Indeed, legumes modify the chemical properties of the entire rhizosphere and, with their own group of specific bacteria, stimulate the rhizosphere for the potential benefit of both the legume and the cereal since their respective root systems are not separate but intermingled (Figure 1).

The intercropped legume rhizosphere also affects bacterial activity via a *priming effect*. Soil organic matter (SOM) decomposition rates are increased by the addition of fresh organic matter from legumes, which stimulates the activities of soil bacteria communities involved in the mineralization of stable SOM (Bernard et al., 2007, 2009; Blagodatskaya and Kuzyakov, 2008; Fontaine et al., 2003). Even if the priming effect has never been measured in legume/cereal intercropping, the pea rhizosphere has been shown to increase the priming effect of the subsequent wheat two-fold (Cheng, 2009). This suggests that intercropping could greatly enhance bacterial SOM mineralization for the benefit of both species (Betencourt, 2012). The role of bacteria in cereal/legume intercropping systems is not fully understood. In order to investigate the key microbial processes involved in intercropped systems in more detail, we now consider the results of investigations on grasslands. This model provides new insights into plant belowground interactions and makes it possible to indirectly underline the relevance of cereal/legume intercropping, which can both enhance plant production and soil bacterial activity.

2.3. Plant diversity and plant production determine microbial activity in grasslands

Investigations on grasslands have demonstrated that plant diversity is significantly correlated with the abundance and diversity of microbial communities. Regardless of the importance of abiotic factors like soil type (Berg and Smalla, 2009; Legay et al., 2014), aboveground plant traits and belowground plant traits have been shown to be responsible for substantial variations in microbial characteristics, with a higher proportion of variation explained by root traits (Legay et al., 2014). For instance, when the site effect was neglected, root dry matter content (RDMC) explained 74,9% of variation in the abundance of ammonia-oxidizing bacteria and 62,1% of variation in the abundance of *Nitrobacter*. Nevertheless, root and leaf traits are closely correlated with, for example, leaf carbon content respectively linked about 39,9%, 35,2%, 50,6% and 49,3%, to the RDMC, specific root length, root carbon content and the root C:N ratio. Stephan et al. (2000) showed that bacterial activity and diversity are stimulated by the presence of specific plant species or functional groups. The legume *Trifolium repens* was found to have the greatest effect on bacterial activity and diversity and was suggested as a key species in plant-microbial interactions, highlighting the interest of taking the functional group of legumes into consideration.

Zak et al. (2003) studied the biomass, activity and composition of microbial community in a long-term field experiment in which plant species richness was controlled. Their results again demonstrated that plant diversity significantly alters the microbial communities present and the

key ecosystem processes they mediate. However, this effect was largely attributable to the increase in overall plant production (Zak et al., 2003). Indeed, it appears that, first and foremost, increased diversity ensures better overall plant production including increased root biomass, and consequently increases soil carbon and nitrogen content, which in turn stimulates microbial activity (Drake, 2003; Grigulis et al., 2013; Spehn et al., 2000; Zak et al., 2003). Such findings highlight the role of complementarity, where promoting different functional groups of plants enables better use of resources, as expressed by higher biomass production and increased flows of materials and energy to the soil (Figure 1; Stephan et al., 2000).

Finally, experiments conducted by Lamb and al. (2010) suggest that regular composition of plant communities over time can strongly influence microbial development, enhance plant-bacterial associations and ensure the establishment of functional microbial groups over the years. It questions the effectiveness of cereal/legume intercropping dynamics when the plants are only associated for one cropping season, while results obtained on grasslands refer to multi-year associations. If grasslands enable greater microbial abundance and activity, thereby emphasizing the relevance of intercropping, further investigations are required to determine the appropriate intercropping design at the appropriate timescale to ensure facilitation and the expression of microbial potential.

2.4. Impact of intercropped legume on arbuscular mycorrhizae (AM)

Previous investigations largely confirmed that arbuscular mycorrhizae can increase the flow of nutrients, plant productivity and ecosystem sustainability (Gianinazzi et al., 2010). AM abundance and diversity are assumed to be linked to plant community diversity (Johnson et al., 2004; van der Heijden et al., 1988; Vandenkoornhuysen et al., 2002). Legumes appear to promote AM colonization in low-input systems. Legumes are known for their tripartite symbiosis (mycorrhiza-legume-*Rhizobium*; Hayman, 1986), and have been shown to be responsible for specific AM colonization, likely due to their specific nutritional requirements linked to the activity of their root nodules (Scheublin et al., 2004; Vandenkoornhuysen et al., 2002). Such specific AM colonization has been confirmed by data showing that secreted legume flavonoids act as a promoter of AM establishment (Siqueira et al., 1991). Using *Medicago* species as model legume, Pivato et al. (2007), showed that the legume enhanced the abundance and diversity of mycorrhizae. Giller and Cadisch (1995) explained this phenomenon by the legumes' dependence upon mycorrhiza for efficient P uptake. This finding on the role of AM in P nutrition is consistent with observations in other intercropping plant models (Ren et al., 2013). The existence of a certain host specificity suggests a recognition process, for instance based on feedback between the plant and the fungus, as proposed by Bever et al. (2003). Following colonization of legumes by AM, their role in promoting growth, nutrient uptake and health has been widely confirmed (Chalk et al., 2006; Gianinazzi et al., 2010; Hayman, 1986; Ortas, 2012). AM have not only been reported to interact with plants but some exchanges have also been observed with bacteria in the rhizosphere. First, cohabitation does not damage colonization by bacteria (Requena et al., 1997; Vázquez et al., 2000). Second, mycorrhizae appear to be a necessary condition for the development of certain strains of bacteria. In the work of Asai (1944) cited in Hayman (1986), in sterilized soil, several legume species failed to nodulate except in soils in which mycorrhizae colonized legume roots.

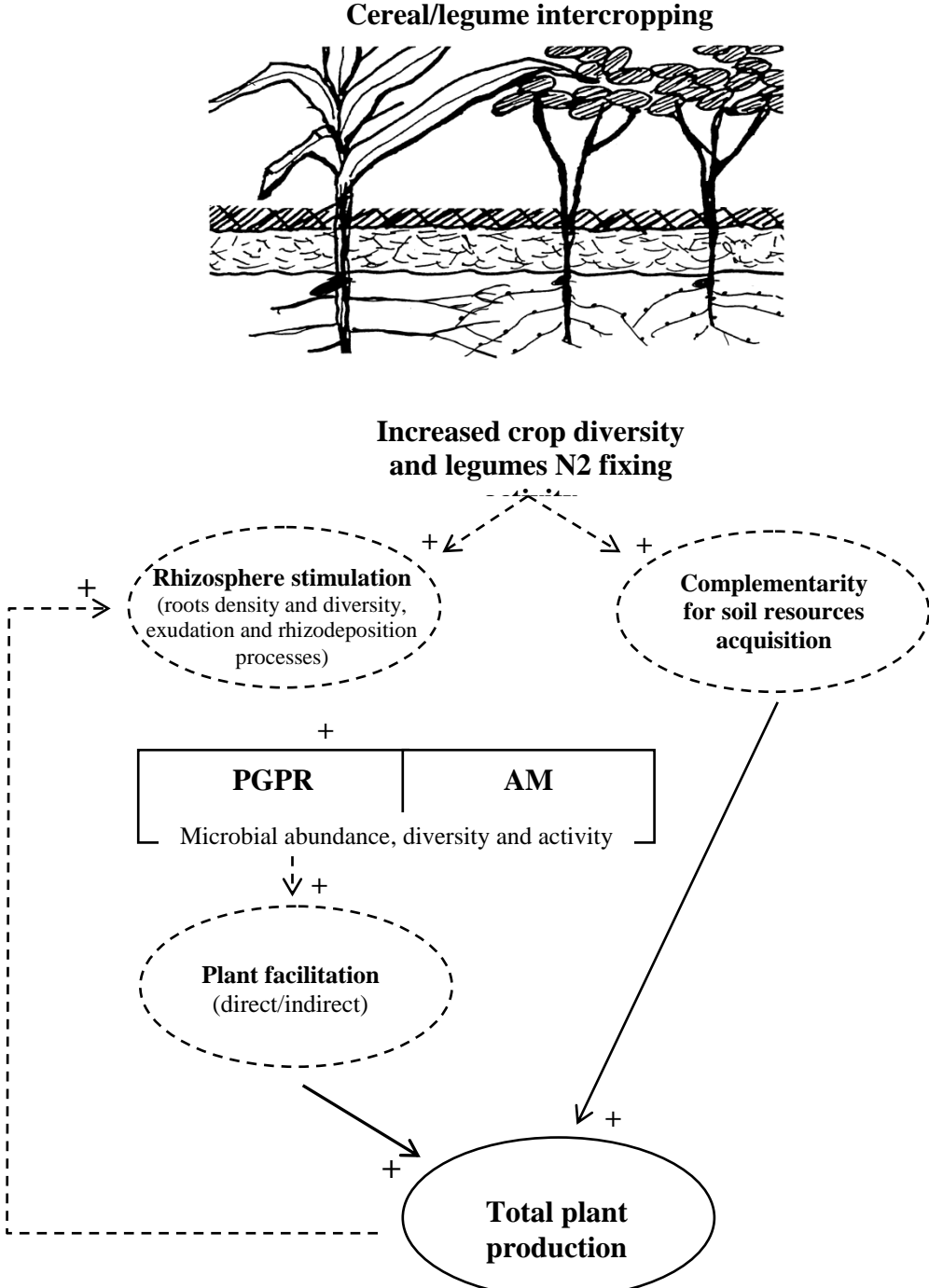
In addition to being a promoter of mycorrhizal colonization, legumes have demonstrated their ability to promote a network of mycorrhizae and to enhance nutrient transfer from one plant to another (Martin et al., 1982; van Kessel et al., 1985), justifying our interest in the facilitation process in which the intercropping system gains from enhanced microbial activity. Indeed, under intercropping, a common mycorrhizal network (CMN) can interconnect individual species or

cultivars by extending AM mycelia from the roots of one plant to those of another (He et al., 2003; Johansen and Jensen, 1996).

In addition to such transfers, both the legume and the cereal benefit from (i) improved soil stability thanks to the binding action of the mycelial network and the secretion of glomalin (Rillig et al., 2002, 2010); (ii) reduced need for fertilizers, since the growth of AM dramatically increases the volume of soil explored for nutrients, particularly P (Kothari et al., 1990, 1991; van der Heijden et al., 1988); (iii) increased plant tolerance to abiotic stresses and protection against biotic stresses (Kennedy and Smith, 1995; Tian et al., 2002).

However, such fungal facilitation is assumed to be context-dependent, and only to occur under favorable conditions (Gianinazzi and Wipf, 2010). As evidenced in field inoculation experiments (Ortas, 2012), monocropping, bulk soil, and the massive use of pesticides and fertilizers represent a serious threat to AM. Thus, despite our lack of thorough knowledge of the mechanisms and processes involved in these plant-AM interactions, cereal/legume intercropping is known to foster such relationships by increasing root density and enriching the soil matrix (Figure 1).

Figure 1. Potential complementarity and facilitation for increased plant production under cereal/legume intercropping



3. Facilitation and microbial activity in cereal/legume intercropping systems: future prospects and challenges in agronomy

3.1. Exploiting the potential of below-ground interactions

It is difficult to understand the consequences in terms of ecosystem functioning from plant diversity increases (Loreau, 2001). In intercropping context, such difficulty is likely linked to the challenge of understanding the changes that occur in an intercropped rhizosphere and to identify both the general mechanisms and the key processes involved in plant-microbe interactions beyond the influence of the field conditions and the specific plant environment.

Nevertheless, intercropping practices are an excellent way to create a context in which favorable belowground interactions can take place and in which intercropped plants influence the soil rhizosphere through their own root activities, exudation and rhizodeposition, and attract particular communities of bacteria and fungi (Berg and Smalla, 2009; Marschner et al., 1986, 2001, 2004). These microbial communities could either be competitors or facilitators. The nature of the resulting microbial interactions will determine the value of the plant association, potentially enhancing plant-microbe trophic relationships and services. The complexification of the rhizosphere appears to entail the diversification of microbial communities that are assumed to optimize rhizosphere ecosystem stability and resilience as well as plant productivity (Czárán et al., 2002; Girvan et al., 2005; Kennedy and Smith, 1995; van der Heijden et al., 2008).

The bacterial genus *Pseudomonas* and *Azospirillum* revealed the ability of different microorganism communities to cohabit, and demonstrated that a diverse bacterial community can substantially benefit plant growth (Couillerot, 2009). The challenge is now to determine the most valuable combination of microorganisms and to ensure their establishment. Indeed, in the case of *Pseudomonas* and *Azospirillum*, Couillerot (2009) found different degrees of *Azospirillum* root colonization depending on the strains used – *A. lipoferum* CRT1, *A. brasilense* UAP-154 or CFN-535, which displayed different degrees of tolerance towards *Pseudomonas* antimicrobial activity (production of diacetyl-phloroglucinol). Moreover, interactions between different communities of microorganisms are not limited to these two bacterial communities but affect the entire rhizosphere community with, for example, the secretion of exopolysaccharide by certain *Pseudomonas* strains, which play a crucial role in the establishment of mycorrhizae (Bianciotto et al., 2001).

Intercropping is assumed to enhance microbial interactions and profit from the stimulated living rhizosphere (increase in plant biomass production, soil organic matter content and nutrient flows; Figure 1). However, overall agroecosystem functioning needs to be taken into account in the management of cereal/legume intercropping. Agroecosystem functioning not only includes a wide range of spatial interactions between plants and soil, but also interactions that take place over time as a function of the developmental stage of the plants and of the microorganisms and of their association dynamics. Given this temporal issue, soil disturbance and intercropping maintenance over time should play a central role in enhancing rhizosphere interactions and facilitation processes.

3.2. Annual intercropping systems are still mainly based on complementarity

The widespread use of cereal/legume intercropping systems usually means associating annual crops for one cropping season. In this form, cereal/legume intercropping has many advantages, most of which are based on better use of environmental resources (Willey, 1990) and on reducing competition thanks to the N₂-fixing activity of legumes (Corre-Hellou et al., 2006). Despite the different rhizosphere interactions induced in intercropping, including facilitative

ones, annual crop management system in which the cover crop is sown and the soil is tilled each year, relies on complementarity mechanisms between intercropped species rather than on significant direct facilitation processes (Bedoussac et al., 2015; Hauggaard-Nielsen et al., 2009). In most systems, the cereal is the main crop, while legumes are expected to use complementary resources (N₂) to grow, and to subsequently improve soil fertility.

For instance, optimizing *temporal* complementarity by using different plant growth dynamics and/or relay-intercropping, i.e. when the cereal and the legume have different growth periods, can enable (i) better growth of the main crop by reducing competition for light and N in the onset stage, (ii) sufficient legume development after the cereal crop is harvested to ensure efficient control of winter weeds and accumulation of N for the following crop (Amossé et al., 2013b). Competitive interactions can also be reduced via several indirect pathways when cereal and legumes are intercropped. The generally enhanced use of light, water and nutrients (N) directly reduce their availability for the growth of weeds, thereby reducing competition with the main crop, or for the development of pests, thereby reducing damage to the crops. However, complementary plant traits for resource acquisition need to be intelligently integrated in the field since unsuitable fertilization practices, e.g. a large P or N supply, can substantially reduce both root exploration and the atmospheric nitrogen fixation rate (Bedoussac and Justes, 2010b; Corre-Hellou et al., 2006; Hinsinger et al., 2011b).

Finally, another advantage of annual cereal/legume intercropping could also be considering the complementarity of yields if a grain legume is used (Iverson et al., 2014). The yield of legume grain could offset a potential decrease in cereal performance. For instance, Bedoussac et al. (2011) found that overall yields of cereal/legume intercropping were 20% to 80% higher than a cereal or a legume cultivated as sole crop, revealing a great production potential.

3.3. Innovative perennial systems should promote potential facilitation interactions

While complementarity mainly relies on morphological and physiological differences in plant traits between species, facilitation interactions in the rhizosphere, especially those involving microorganisms, require the establishment of a biologically complex rhizosphere ecosystem. However, it is assumed that such biological complexification and ecological functions improvement in soil nutrients fluxes require time and avoid disturbing the soil (Crews et al., 2016). Promoting facilitation processes and microbial activity in the long term thus implies taking the whole agroecosystem into consideration and finding strategies that break with the usual concept of an annual cropping system defined by the final performance of one crop, and with the use of approaches focused on short-term outcomes and immediate considerations.

Indeed, plant interactions and soil activity achieve a higher degree of efficiency and intensity in perennial systems, such as grasslands, which tend to be close to natural ecosystems capable of successional changes that create and strengthen regulation and feedback processes (Crews et al., 2016). This perennial perspective underlines the major limitation of annual cereal/legume intercropping, which is a time-limited association between plants, where tillage maintains the agroecosystem in an early succession stage that is less biologically complex and regulated (Smith, 2015). For instance, the synchrony between nutrient supply and crop demand, especially in the case of nitrogen, is currently uncertain since only a fraction of legume nitrogen is recovered by crops (Crews and Peoples, 2005). Innovative systems have been proposed including perennial intercropping with a permanent cover crop, direct seeding, living-mulch systems, and intercropping with a perennial legume. These systems have produced promising results in which soil structure, carbon storage, plant biomass, nutrient cycles as well as the abundance and activity of soil organisms were improved (Autret et al., 2016; Chantigny et al., 1997; Henneron et al., 2015; Zhang et al., 2011). Despite the major agronomic challenges that need to be overcome like establishment costs, market opportunities for the crops, and delayed

benefits (Snapp et al., 1998), research on these innovative perennial intercropping systems remains largely insufficient. More recent research programs concern the domestication and breeding of perennial grains (Cox et al., 2002, 2006; DeHaan et al., 2014; Gazza et al., 2015), suggesting growing interest and knowledge in perennial approaches. In the case of perennial grains, intercropping with a legume could be an option, as it would enhance facilitative roots and microbial processes and ensure a more stable agroecosystem, closer to that of grasslands.

3.4. Research prospects and future investigations

Cereal/legume intercropping aims to improve the efficiency of the entire agroecosystem from both ecological and economic points of view (Altieri, 2000; Pelzer et al., 2012; Vandermeer, 1992; Wezel et al., 2014). However the success of this agroecological practice depends to a great extent on local field conditions and is still threatened by competition between intercropped species, particularly when influenced by unfavorable local climate, growth conditions, fertilization practices or choice of species (Hauggaard-Nielsen and Jensen, 2005). Despite the fact that the influence of facilitation interactions is assumed to be significant, this influence is not clearly apparent in the variability of results from investigations of the rhizosphere ecosystem. We thus recommend that future research should begin by investigating the microbial communities, identifying functional groups of genera, their role and their preferential affinity for specific plant associations as well as the dynamics of their facilitation process which appears to be the weak point in annual intercropping systems. Increasing attention should be paid to innovative systems that include perennial system with the aim of changing the nature of the intercropping system itself, including a greater degree of ecological intensification and regulation.

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