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

Olivier Duchene, Jean-François Vian, Florian Celette

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

Olivier DUCHENE*, Jean-François VIAN, Florian CELETTE

ISARA-Lyon (member of the University of Lyon), Department of Agroecology and Environment, 23 rue Jean Baldassini, 69364 Lyon cedex 07, France

*Corresponding author : Phone.: +33 (0)4 27 85 85 91
E-mail: olduchene@isara.fr (O. Duchene) fcelette@isara.fr (F. Celette) jvian@isara.fr (J.F. Vian)

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**	- Higher intercropping yields than for sole crop in low-input systems *(LER up to 2,2)*	(Bedoussac and Justes, 2010a; Bergkvist et al., 2011; Hauggaard-Nielsen et al., 2008; Jensen et al., 2006; Willey, 1979)
		- Maintained or increased yield and quality through increased grain protein content *(up to 1% increase)*	(Bedoussac et al., 2011; Hauggaard-Nielsen et al., 2008; Justes et al., 2009; Pelzer et al., 2012)
	Nitrogen dynamics	- 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	- Better overall exploration of resources - Improved resource use efficiency *(light, nitrogen, water use efficiency improved up to 20%)*	(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**	- 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	- Reduced attacks and damage caused by pests *(up to 50% of pest species reduced)*	(Ratnadass et al., 2012; Risch, 1983; Smith and McSorley, 2000; Trenbath, 1993)
	Soil	- 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 positives 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 positives 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 17,7g N m^2 when pea was grown as intercropped species with barley whereas it was only 5,1 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 ^{15}N-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 N_2 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 N_2 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)

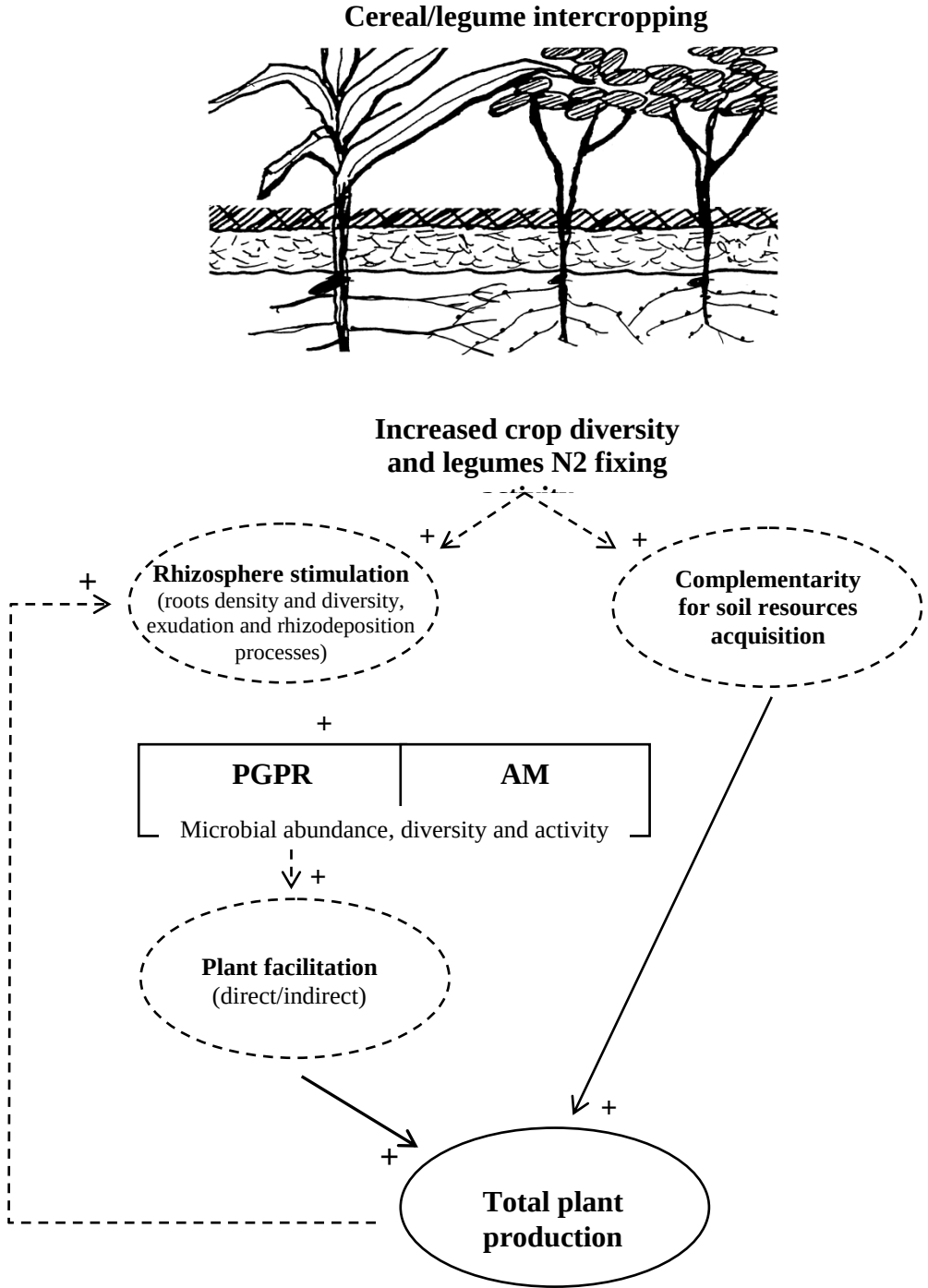
Previous investigations largely confirmed that arbuscular mycorrhizae can increase the flow of nutrients, plant productivity and ecosystem sustainability (Gianinazzi et al., 2010). AM abundance and diversity are assumed to be linked to plant community diversity (Johnson et al., 2004; van der Heijden et al., 1988; Vandenkoornhuyse 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; Vandenkoornhuyse 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 N_2-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 (N_2) to grow, and to subsequently improve soil fertility.

For instance, optimizing *temporal c*omplementarity 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.

Acknowledgments

The authors greatfully acknowledge D. Goodfellow for revising the text in English. This research received no funding from public, commercial, or not-for-profit agencies. The study was conducted as part of the CASDAR program Alliance (n°5376), and ANR program LEGITIMES (ANR-13-AGRO-0004).

References

Ahmad, I. (Ed.), 2008. Plant-bacteria interactions: strategies and techniques to promote plant growth. Wiley-VCH-Verl, Weinheim.

Altieri, M.A., 2000. Agroecology: principles and strategies for designing sustainable farming systems. Agroecol. Innov. 40–46.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agric. Ecosyst. Environ. 74, 19–31.

Alvey, S., Yang, C.-H., Buerkert, A., Crowley, D.E., 2003. Cereal/legume rotation effects on rhizosphere bacterial community structure in west african soils. Biol. Fertil. Soils 37, 73–82. doi:10.1007/s00374-002-0573-2

Amossé, C., Jeuffroy, M.-H., Celette, F., David, C., 2013a. Relay-intercropped forage legumes help to control weeds in organic grain production. Eur. J. Agron. 49, 158–167. doi:10.1016/j.eja.2013.04.002

Amossé, C., Jeuffroy, M.-H., David, C., 2013b. Relay intercropping of legume cover crops in organic winter wheat: Effects on performance and resource availability. Field Crops Res. 145, 78–87. doi:10.1016/j.fcr.2013.02.010

Amossé, C., Jeuffroy, M.-H., Mary, B., David, C., 2014. Contribution of relay intercropping with legume cover crops on nitrogen dynamics in organic grain systems. Nutr. Cycl. Agroecosystems 98, 1–14. doi:10.1007/s10705-013-9591-8

Anil, Park, Phipps, Miller, 1998. Temperate intercropping of cereals for forage: a review of the potential for growth and utilization with particular reference to the UK. Grass Forage Sci. 53, 301–317. doi:10.1046/j.1365-2494.1998.00144.x

Asai, T.V., 1944. Uber die Mykorrhizenbildung der leguminosen Pflanzen. Jap J Bot 13, 463–485.

Audenaert, K., Pattery, T., Cornelis, P., Höfte, M., 2002. Induction of Systemic Resistance to Botrytis cinerea in Tomato by Pseudomonas aeruginosa 7NSK2: Role of Salicylic Acid, Pyochelin, and Pyocyanin. Mol. Plant. Microbe Interact. 15, 1147–1156. doi:10.1094/MPMI.2002.15.11.1147

Autret, B., Mary, B., Chenu, C., Balabane, M., Girardin, C., Bertrand, M., Grandeau, G., Beaudoin, N., 2016. Alternative arable cropping systems: A key to increase soil organic carbon storage? Results from a 16 year field experiment. Agric. Ecosyst. Environ. 232, 150–164. doi:10.1016/j.agee.2016.07.008

Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere intercations with plants and other organisms. Annu. Rev. Plant Biol. 57, 233–266. doi:10.1146/annurev.arplant.57.032905.105159

Banik, P., Midya, A., Sarkar, B.K., Ghose, S.S., 2006. Wheat and chickpea intercropping systems in an additive series experiment: Advantages and weed smothering. Eur. J. Agron. 24, 325–332. doi:10.1016/j.eja.2005.10.010

Bargaz, A., Isaac, M.E., Jensen, E.S., Carlsson, G., 2015a. Intercropping of Faba Bean with Wheat Under Low Water Availability Promotes Faba Bean Nodulation and Root Growth in Deeper Soil Layers. Procedia Environ. Sci., Agriculture and Climate Change - Adapting Crops to Increased Uncertainty (AGRI 2015) 29, 111–112. doi:10.1016/j.proenv.2015.07.188

Bargaz, A., Zaman-Allah, M., Farissi, M., Lazali, M., Drevon, J.-J., Maougal, R.T., Georg, C., 2015b. Physiological and Molecular Aspects of Tolerance to Environmental Constraints in Grain and Forage Legumes. Int. J. Mol. Sci. 16, 18976–19008. doi:10.3390/ijms160818976

Bartelt-Ryser, J., Joshi, J., Schmid, B., Brandl, H., Balser, T., 2005. Soil feedbacks of plant diversity on soil microbial communities and subsequent plant growth. Perspect. Plant Ecol. Evol. Syst. 7, 27–49. doi:10.1016/j.ppees.2004.11.002

Bashan, Y., de-Bashan, L.E., 2010. How the Plant Growth-Promoting Bacterium Azospirillum Promotes Plant Growth—A Critical Assessment, in: Advances in Agronomy. Elsevier, pp. 77–136.

Bedoussac, L., 2009. Analyse du fonctionnement des performances des associations blé dur-pois d'hiver et blé dur-féverole d'hiver pour la conception d'itinéraires techniques adaptés à différents objectifs de production en systèmes bas-intrants.

Bedoussac, L., Journet, E.-P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E.S., Prieur, L., Justes, E., 2015. Ecological principles underlying the increase of productivity achieved by cereal-grain legume intercrops in organic farming. A review. Agron. Sustain. Dev. 35, 911–935. doi:10.1007/s13593-014-0277-7

Bedoussac, L., Journet, E.-P., Rouet, P., Josse, C., Ledoux, S., Justes, E., 2011. Cultiver du blé (dur ou tendre) en association avec une légumineuse à graine: un moyen efficace pour accroitre la production et la qualité des graines en agriculture biologique.

Bedoussac, L., Justes, E., 2010a. The efficiency of a durum wheat-winter pea intercrop to improve yield and wheat grain protein concentration depends on N availability during early growth. Plant Soil 330, 19–35. doi:10.1007/s11104-009-0082-2

Bedoussac, L., Justes, E., 2010b. Dynamic analysis of competition and complementarity for light and N use to understand the yield and the protein content of a durum wheat–winter pea intercrop. Plant Soil 330, 37–54. doi:10.1007/s11104-010-0303-8

Berg, G., Smalla, K., 2009. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiol. Ecol. 68, 1–13. doi:10.1111/j.1574-6941.2009.00654.x

Bergkvist, G., Stenberg, M., Wetterlind, J., Båth, B., Elfstrand, S., 2011. Clover cover crops under-sown in winter wheat increase yield of subsequent spring barley—Effect of N dose and companion grass. Field Crops Res. 120, 292–298. doi:10.1016/j.fcr.2010.11.001

Bernard, L., Maron, P.A., Mougel, C., Nowak, V., Lévêque, J., Marol, C., Balesdent, J., Gibiat, F., Ranjard, L., 2009. Contamination of Soil by Copper Affects the Dynamics, Diversity, and Activity of Soil Bacterial Communities Involved in Wheat Decomposition and Carbon Storage. Appl. Environ. Microbiol. 75, 7565–7569. doi:10.1128/AEM.00616-09

Bernard, L., Mougel, C., Maron, P.-A., Nowak, V., Lévêque, J., Henault, C., Haichar, F. el Z., Berge, O., Marol, C., Balesdent, J., Gibiat, F., Lemanceau, P., Ranjard, L., 2007. Dynamics and identification of soil microbial populations actively assimilating carbon from 13C-labelled wheat residue as estimated by DNA- and RNA-SIP techniques. Environ. Microbiol. 9, 752–764. doi:10.1111/j.1462-2920.2006.01197.x

Bertin, C., Yang, X., Weston, L.A., 2003. The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 256, 67–83. doi:10.1023/A:1026290508166

Betencourt, E., 2012. Interactions entre céréale et légumineuse en association et acquisition de phosphore du sol: processus rhizosphériques sous-jacents. Montpellier SupAgro.

Bever, J.D., Pringle, A., Schultz, P.A., 2003. Dynamics within the Plant — Arbuscular Mycorrhizal Fungal Mutualism: Testing the Nature of Community Feedback, in: Heijden, D.M.G.A. van der, Sanders, D.I.R. (Eds.), Mycorrhizal Ecology, Ecological Studies. Springer Berlin Heidelberg, pp. 267–292. doi:10.1007/978-3-540-38364-2_11

Bianciotto, V., Andreotti, S., Balestrini, R., Bonfante, P., Perotto, S., 2001. Mucoid Mutants of the Biocontrol Strain Pseudomonas fluorescens CHA0 Show Increased Ability in Biofilm Formation on Mycorrhizal and Nonmycorrhizal Carrot Roots. Mol. Plant. Microbe Interact. 14, 255–260. doi:10.1094/MPMI.2001.14.2.255

Blagodatskaya, E., Kuzyakov, Y., 2008. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. Biol. Fertil. Soils 45, 115–131. doi:10.1007/s00374-008-0334-y

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. J. Ecol. 96, 18–34. doi:10.1111/j.1365-2745.2007.01295.x

Brussaard, L., de Ruiter, P.C., Brown, G.G., 2007. Soil biodiversity for agricultural sustainability. Agric. Ecosyst. Environ. 121, 233–244. doi:10.1016/j.agee.2006.12.013

Cahill, J.F., McNickle, G.G., Haag, J.J., Lamb, E.G., Nyanumba, S.M., St. Clair, C.C., 2010. Plants Integrate Information About Nutrients and Neighbors. Science 328, 1657–1657. doi:10.1126/science.1189736

Callaway, R.M., 1995. Positive interactions among plants. Bot. Rev. 61, 306–349. doi:10.1007/BF02912621

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–848. doi:10.1038/nature00812

Carof, M., 2006. Fonctionnement de peuplements en semis direct associant du blé tendre d'hiver (Triticum aestivum L.) à différentes plantes de couverture en climat tempéré. INAPG (AgroParisTech).

Chalk, P.M., Souza, R. de F., Urquiaga, S., Alves, B.J.R., Boddey, R.M., 2006. The role of arbuscular mycorrhiza in legume symbiotic performance. Soil Biol. Biochem. 38, 2944–2951. doi:10.1016/j.soilbio.2006.05.005

Chantigny, M.H., Angers, D.A., Prévost, D., Vézina, L.-P., Chalifour, F.-P., 1997. Soil Aggregation and Fungal and Bacterial Biomass under Annual and Perennial Cropping Systems. Soil Sci. Soc. Am. J. 61, 262. doi:10.2136/sssaj1997.03615995006100010037x

Cheng, W., 2009. Rhizosphere priming effect: Its functional relationships with microbial turnover, evapotranspiration, and C–N budgets. Soil Biol. Biochem. 41, 1795–1801. doi:10.1016/j.soilbio.2008.04.018

Clergue, B., Amiaud, B., Pervanchon, F., Lasserre-Joulin, F., Plantureux, S., 2005. Biodiversity: function and assessment in agricultural areas. A review. Agron. Sustain. Dev. 25, 1–15. doi:10.1051/agro:2004049

Compant, S., Clément, C., Sessitsch, A., 2010. Plant growth-promoting bacteria in the rhizo-and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. Soil Biol. Biochem. 42, 669–678.

Corre-Hellou, G., 2005. Acquisition de l'azote dans des associations pois - orge (Pisum sativum L. - Hordeum vulgare L.) en relation avec le fonctionnement du peuplement. Angers.

Corre-Hellou, G., Dibet, A., Hauggaard-Nielsen, H., Crozat, Y., Gooding, M., Ambus, P., Dahlmann, C., von Fragstein, P., Pristeri, A., Monti, M., Jensen, E.S., 2011. The competitive ability of pea–barley intercrops against weeds and the interactions with crop productivity and soil N availability. Field Crops Res. 122, 264–272. doi:10.1016/j.fcr.2011.04.004

Corre-Hellou, G., Fustec, J., Crozat, Y., 2006. Interspecific Competition for Soil N and its Interaction with N2 Fixation, Leaf Expansion and Crop Growth in Pea–Barley Intercrops. Plant Soil 282, 195–208. doi:10.1007/s11104-005-5777-4

Couillerot, O., 2009. Compatibilité des bactéries phytobénéfiques Azospirillum et Pseudomonas dans la rhizosphère. Université Claude Bernard-Lyon I.

Cox, T.S., Bender, M., Picone, C., Tassel, D.V., Holland, J.B., Brummer, E.C., Zoeller, B.E., Paterson, A.H., Jackson, W., 2002. Breeding perennial grain crops. Crit. Rev. Plant Sci. 21, 59–91.

Cox, T.S., Glover, J.D., Tassel, D.L.V., Cox, C.M., DeHaan, L.R., 2006. Prospects for Developing Perennial Grain Crops. BioScience 56, 649–659. doi:10.1641/0006-3568(2006)56[649:PFDPGC]2.0.CO;2

Crews, T.E., Blesh, J., Culman, S.W., Hayes, R.C., Jensen, E.S., Mack, M.C., Peoples, M.B., Schipanski, M.E., 2016. Going where no grains have gone before: From early to mid-succession. Agric. Ecosyst. Environ. 223, 223–238. doi:10.1016/j.agee.2016.03.012

Crews, T.E., Peoples, M.B., 2005. Can the Synchrony of Nitrogen Supply and Crop Demand be Improved in Legume and Fertilizer-based Agroecosystems? A Review. Nutr. Cycl. Agroecosystems 72, 101–120. doi:10.1007/s10705-004-6480-1

Cu, S.T.T., Hutson, J., Schuller, K.A., 2005. Mixed culture of wheat (Triticum aestivum L.) with white lupin (Lupinus albus L.) improves the growth and phosphorus nutrition of the wheat. Plant Soil 272, 143–151. doi:10.1007/s11104-004-4336-8

Czárán, T.L., Hoekstra, R.F., Pagie, L., 2002. Chemical warfare between microbes promotes biodiversity. Proc. Natl. Acad. Sci. 99, 786–790.

Dakora, F.D., Phillips, D.A., 2002. Root exudates as mediators of mineral acquisition in low-nutrient environments. Plant Soil 245, 35–47. doi:10.1023/A:1020809400075

Degens, B.P., Schipper, L.A., Sparling, G.P., Vojvodic-Vukovic, M., 2000. Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities. Soil Biol. Biochem. 32, 189–196. doi:10.1016/S0038-0717(99)00141-8

DeHaan, L., Wang, S., Larson, S., Cattani, D., Zhang, X., Viinanen, T., 2014. Current efforts to develop perennial wheat and domesticate Thinopyrum intermedium as a perennial grain. Meet. Abstr.

Doelsch, E., Pellerin, S., Capillon, A., Martin-Garin, A., Dorioz, J.-M., Gerard, F., n.d. Modélisation mécaniste des interactions rhizosphériques déterminant la facilitation d'acquisition du phosphore en association céréale-légumineuse.

Drake, J.M., 2003. Why does grassland productivity increase with species richness? Disentangling species richness and composition with tests for overyielding and superyielding in biodiversity experiments. Proc. R. Soc. Lond. B Biol. Sci. 270, 1713–1719. doi:10.1098/rspb.2003.2423

Drogue, B., 2013. Spécificité de la coopération phytostimulatrice Azospirillum-céréales. Université Claude Bernard-Lyon I.

Faure, D., Vereecke, D., Leveau, J.H.J., 2009. Molecular communication in the rhizosphere. Plant Soil 321, 279–303. doi:10.1007/s11104-008-9839-2

Fontaine, S., Mariotti, A., Abbadie, L., 2003. The priming effect of organic matter: a question of microbial competition? Soil Biol. Biochem. 35, 837–843. doi:10.1016/S0038-0717(03)00123-8

Fridley, J.D., 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. Oecologia 132, 271–277. doi:10.1007/s00442-002-0965-x

Fridley, J.D., 2001. The influence of species diversity on ecosystem productivity: how, where, and why? Oikos 93, 514–526.

Fustec, J., Lesuffleur, F., Mahieu, S., Cliquet, J.-B., 2010. Nitrogen rhizodeposition of legumes. A review. Agron. Sustain. Dev. 30, 57–66. doi:10.1051/agro/2009003

Gazza, L., Galassi, E., Ciccoritti, R., Cacciatori, P., Pogna, N.E., 2015. Qualitative traits of perennial wheat lines derived from different Thinopyrum species. Genet. Resour. Crop Evol. 63, 209–219. doi:10.1007/s10722-015-0240-8

Gianinazzi, S., Gollotte, A., Binet, M.-N., van Tuinen, D., Redecker, D., Wipf, D., 2010. Agroecology: the key role of arbuscular mycorrhizas in ecosystem services. Mycorrhiza 20, 519–530. doi:10.1007/s00572-010-0333-3

Gianinazzi, S., Wipf, D., 2010. Des champignons au service des plantes. PHM–Revue Hortic. 521, 9–11.

Giller, K.E., Cadisch, G., 1995. Future benefits from biological nitrogen fixation: An ecological approach to agriculture, in: Ladha, J.K., Peoples, M.B. (Eds.), Management of Biological Nitrogen Fixation for the Development of More Productive and Sustainable Agricultural Systems, Developments in Plant and Soil Sciences. Springer Netherlands, pp. 255–277. doi:10.1007/978-94-011-0055-7_13

Giller, K.E., Ormesher, J., Awah, F.M., 1991. Nitrogen transfer from Phaseolus bean to intercropped maize measured using 15N-enrichment and 15N-isotope dilution methods. Soil Biol. Biochem. 23, 339–346. doi:10.1016/0038-0717(91)90189-Q

Girvan, M.S., Campbell, C.D., Killham, K., Prosser, J.I., Glover, L.A., 2005. Bacterial diversity promotes community stability and functional resilience after perturbation. Environ. Microbiol. 7, 301–313. doi:10.1111/j.1462-2920.2005.00695.x

Gliessman, S.R., 1990. Agroecology: Researching the Ecological Basis for Sustainable Agriculture, in: Gliessman, S.R. (Ed.), Agroecology, Ecological Studies. Springer New York, pp. 3–10. doi:10.1007/978-1-4612-3252-0_1

Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., Kastl, E., Arnoldi, C., Bardgett, R.D., Poly, F., Pommier, T., Schloter, M., Tappeiner, U., Bahn, M., Clément, J.-C., 2013. Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. J. Ecol. 101, 47–57. doi:10.1111/1365-2745.12014

Hamilton, E.W., Frank, D.A., 2001. Can plants stimulate soil microbes and their own nutrient supply? evidence from a grazing tolerant grass. Ecology 82, 2397–2402. doi:10.1890/0012-9658(2001)082[2397:CPSSMA]2.0.CO;2

Hauggaard-Nielsen, H., Ambus, P., Jensen, E.S., 2001a. Temporal and spatial distribution of roots and competition for nitrogen in pea-barley intercrops – a field study employing 32P technique. Plant Soil 236, 63–74. doi:10.1023/A:1011909414400

Hauggaard-Nielsen, H., Ambus, P., Jensen, E.S., 2001b. Interspecific competition, N use and interference with weeds in pea–barley intercropping. Field Crops Res. 70, 101–109. doi:10.1016/S0378-4290(01)00126-5

Hauggaard-Nielsen, H., Gooding, M., Ambus, P., Corre-Hellou, G., Crozat, Y., Dahlmann, C., Dibet, A., von Fragstein, P., Pristeri, A., Monti, M., Jensen, E.S., 2009. Pea–barley intercropping for efficient symbiotic N2-fixation, soil N acquisition and use of other nutrients in European organic cropping systems. Field Crops Res. 113, 64–71. doi:10.1016/j.fcr.2009.04.009

Hauggaard-Nielsen, H., Jensen, E.S., 2005. Facilitative Root Interactions in Intercrops. Plant Soil 274, 237–250. doi:10.1007/s11104-004-1305-1

Hauggaard-Nielsen, H., Jørnsgaard, B., Kinane, J., Jensen, E.S., 2008. Grain legume–cereal intercropping: The practical application of diversity, competition and facilitation in arable and organic cropping systems. Renew. Agric. Food Syst. 23, 3–12. doi:10.1017/S1742170507002025

Hayman, D.S., 1986. Mycorrhizae of nitrogen-fixing legumes. MIRCEN J. 2, 121–145.

He, X.-H., Critchley, C., Bledsoe, C., 2003. Nitrogen Transfer Within and Between Plants Through Common Mycorrhizal Networks (CMNs). Crit. Rev. Plant Sci. 22, 531–567. doi:10.1080/713608315

Henneron, L., Bernard, L., Hedde, M., Pelosi, C., Villenave, C., Chenu, C., Bertrand, M., Girardin, C., Blanchart, E., 2015. Fourteen years of evidence for positive effects of conservation agriculture and organic farming on soil life. Agron. Sustain. Dev. 35, 169–181. doi:10.1007/s13593-014-0215-8

Hinsinger, P., 2001. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant Soil 237, 173–195. doi:10.1023/A:1013351617532

Hinsinger, P., Bengough, A.G., Vetterlein, D., Young, I.M., 2009. Rhizosphere: biophysics, biogeochemistry and ecological relevance. Plant Soil 321, 117–152. doi:10.1007/s11104-008-9885-9

Hinsinger, P., Betencourt, E., Bernard, L., Brauman, A., Plassard, C., Shen, J., Tang, X., Zhang, F., 2011a. P for Two, Sharing a Scarce Resource: Soil Phosphorus Acquisition in the Rhizosphere of Intercropped Species. Plant Physiol. 156, 1078–1086. doi:10.1104/pp.111.175331

Hinsinger, P., Brauman, A., Devau, N., Gérard, F., Jourdan, C., Laclau, J.-P., Le Cadre, E., Jaillard, B., Plassard, C., 2011b. Acquisition of phosphorus and other poorly mobile nutrients by roots. Where do plant nutrition models fail? Plant Soil 348, 29–61. doi:10.1007/s11104-011-0903-y

Hinsinger, P., Plassard, C., Tang, C., Jaillard, B., 2003. Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. Plant Soil 248, 43–59. doi:10.1023/A:1022371130939

Hirsch, A.M., Bauer, W.D., Bird, D.M., Cullimore, J., Tyler, B., Yoder, J.I., 2003. Molecular signals and receptors: controlling rhizosphere interactions between plants and other organisms. Ecology 84, 858–868. doi:10.1890/0012-9658(2003)084[0858:MSARCR]2.0.CO;2

Hodge, A., 2009. Root decisions. Plant Cell Environ. 32, 628–640. doi:10.1111/j.1365-3040.2008.01891.x

Iverson, A.L., Marín, L.E., Ennis, K.K., Gonthier, D.J., Connor-Barrie, B.T., Remfert, J.L., Cardinale, B.J., Perfecto, I., 2014. REVIEW: Do polycultures promote win-wins or trade-offs in agricultural ecosystem services? A meta-analysis. J. Appl. Ecol. 51, 1593–1602. doi:10.1111/1365-2664.12334

Jain, V., Gupta, K., 2003. The flavonoid naringenin enhances intercellular colonization of rice roots by Azorhizobium caulinodans. Biol. Fertil. Soils 38, 119–123. doi:10.1007/s00374-003-0599-0

Jeffries, P., Gianinazzi, S., Perotto, S., Turnau, K., Barea, J.-M., 2003. The contribution of arbuscular mycorrhizal fungi in sustainable maintenance of plant health and soil fertility. Biol. Fertil. Soils 37, 1–16.

Jensen, E.S., 1996. Grain yield, symbiotic N2 fixation and interspecific competition for inorganic N in pea-barley intercrops. Plant Soil 182, 25–38. doi:10.1007/BF00010992

Johansen, A., Jensen, E.S., 1996. Transfer of N and P from intact or decomposing roots of pea to barley interconnected by an arbuscular mycorrhizal fungus. Soil Biol. Biochem. 28, 73–81. doi:10.1016/0038-0717(95)00117-4

Johansson, J.F., Paul, L.R., Finlay, R.D., 2004. Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. FEMS Microbiol. Ecol. 48, 1–13. doi:10.1016/j.femsec.2003.11.012

Johnson, D., Vandenkoornhuyse, P.J., Leake, J.R., Gilbert, L., Booth, R.E., Grime, J.P., Young, J.P.W., Read, D.J., 2004. Plant communities affect arbuscular mycorrhizal fungal diversity and community composition in grassland microcosms. New Phytol. 161, 503–515. doi:10.1046/j.1469-8137.2003.00938.x

Justes, E., Bedoussac, L., Corre-Hellou, G., Fustec, J., Hinsinger, P., Jeuffroy, M.-H., Journet, E.-P., Louarn, G., Naudin, C., Pelzer, E., 2014. Les processus de complémentarité de niche et de facilitation déterminent le fonctionnement des associations végétales et leur efficacité pour l'acquisition des ressources abiotiques. Innov. Agron. 1–24.

Kennedy, A.C., Smith, K.L., 1995. Soil microbial diversity and the sustainability of agricultural soils. Plant Soil 170, 75–86.

Kothari, S.K., Marschner, H., Römheld, V., 1991. Contribution of the VA mycorrhizal hyphae in acquisition of phosphorus and zinc by maize grown in a calcareous soil. Plant Soil 131, 177–185.

Kothari, S.K., Marschner, H., Römheld, V., 1990. Direct and indirect effects of VA mycorrhizal fungi and rhizosphere microorganisms on acquisition of mineral nutrients by maize (Zea mays L.) in a calcareous soil. New Phytol. 116, 637–645.

Lambers, H., Shane, M.W., Cramer, M.D., Pearse, S.J., Veneklaas, E.J., 2006. Root Structure and Functioning for Efficient Acquisition of Phosphorus: Matching Morphological and Physiological Traits. Ann. Bot. 98, 693–713. doi:10.1093/aob/mcl114

Latati, M., Bargaz, A., Belarbi, B., Lazali, M., Benlahrech, S., Tellah, S., Kaci, G., Drevon, J.J., Ounane, S.M., 2016. The intercropping common bean with maize improves the rhizobial efficiency, resource use and grain yield under low phosphorus availability. Eur. J. Agron. 72, 80–90. doi:10.1016/j.eja.2015.09.015

Latati, M., Blavet, D., Alkama, N., Laoufi, H., Drevon, J.J., Gérard, F., Pansu, M., Ounane, S.M., 2014. The intercropping cowpea-maize improves soil phosphorus availability and maize yields in an alkaline soil. Plant Soil 385, 181–191. doi:10.1007/s11104-014-2214-6

Latif, M.A., Mehuys, G.R., Mackenzie, A.F., Alli, I., Faris, M.A., 1992. Effects of legumes on soil physical quality in a maize crop. Plant Soil 140, 15–23. doi:10.1007/BF00012802

Legay, N., Baxendale, C., Grigulis, K., Krainer, U., Kastl, E., Schloter, M., Bardgett, R.D., Arnoldi, C., Bahn, M., Dumont, M., Poly, F., Pommier, T., Clement, J.C., Lavorel, S., 2014. Contribution of above- and below-ground plant traits to the structure and function of grassland soil microbial communities. Ann. Bot. 114, 1011–1021. doi:10.1093/aob/mcu169

Lemanceau, P., 1992. Effets bénéfiques de rhizobactéries sur les plantes: exemple des Pseudomonas spp fluorescents. Agronomie 12, 413–437.

Lemanceau, P., Maron, P.-A., Mazurier, S., Mougel, C., Philippot, L., Pivato, B., Plassart, P., Ranjard, L., Revellin, C., Tardy, V., others, 2014. Qu'attendre des recherches en microbiologie du sol?, in: Fertilisation et environnement: Quelles pistes pour l'aide à la décision? p. 290.

Li, H., Shen, J., Zhang, F., Clairotte, M., Drevon, J.J., Cadre, E.L., Hinsinger, P., 2007. Dynamics of phosphorus fractions in the rhizosphere of common bean (Phaseolus vulgaris L.) and durum wheat (Triticum turgidum durum L.) grown in monocropping and intercropping systems. Plant Soil 312, 139–150. doi:10.1007/s11104-007-9512-1

Li, H., Shen, J., Zhang, F., Marschner, P., Cawthray, G., Rengel, Z., 2009. Phosphorus uptake and rhizosphere properties of intercropped and monocropped maize, faba bean, and white lupin in acidic soil. Biol. Fertil. Soils 46, 79–91. doi:10.1007/s00374-009-0411-x

Li, L., Tilman, D., Lambers, H., Zhang, F.-S., 2014. Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. New Phytol. 203, 63–69. doi:10.1111/nph.12778

Li, L., Zhang, F., Li, X., Christie, P., Sun, J., Yang, S., Tang, C., 2003. Interspecific facilitation of nutrient uptake by intercropped maize and faba bean. Nutr. Cycl. Agroecosystems 65, 61–71. doi:10.1023/A:1021885032241

Li, S.M., Li, L., Zhang, F.S., Tang, C., 2004. Acid Phosphatase Role in Chickpea/Maize Intercropping. Ann. Bot. 94, 297–303. doi:10.1093/aob/mch140

Loreau, M., 2001. Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model. Proc. R. Soc. Lond. B Biol. Sci. 268, 303–309. doi:10.1098/rspb.2000.1366

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.

Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J. Ecol. 97, 199–205. doi:10.1111/j.1365-2745.2008.01476.x

Mahieu, S., 2009. Assessment of the below ground contribution of field grown pea (Pisum sativum L.) to the soil N pool. Citeseer.

Mahieu, S., Escarré, J., Brunel, B., Méjamolle, A., Soussou, S., Galiana, A., Cleyet-Marel, J.-C., 2014. Soil nitrogen balance resulting from N fixation and rhizodeposition by the symbiotic association Anthyllis vulneraria/Mesorhizobium metallidurans grown in highly polluted Zn, Pb and Cd mine tailings. Plant Soil 375, 175–188. doi:10.1007/s11104-013-1941-4

Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts, tools and models. A review. Agron. Sustain. Dev. 29, 43–62. doi:10.1051/agro:2007057

Marschner, H., Römheld, V., Horst, W.J., Martin, P., 1986. Root-induced changes in the rhizosphere: Importance for the mineral nutrition of plants. Z. Für Pflanzenernähr. Bodenkd. 149, 441–456. doi:10.1002/jpln.19861490408

Marschner, P., Crowley, D., Yang, C.H., 2004. Development of specific rhizosphere bacterial communities in relation to plant species, nutrition and soil type. Plant Soil 261, 199–208.

Marschner, P., Yang, C.-H., Lieberei, R., Crowley, D.E., 2001. Soil and plant specific effects on bacterial community composition in the rhizosphere. Soil Biol. Biochem. 33, 1437–1445. doi:10.1016/S0038-0717(01)00052-9

Martin, M.P.L.D., Snaydon, R.W., Drennan, D.S.H., 1982. Lithium as a non-radioactive tracer for roots of intercropped species. Plant Soil 64, 203–208. doi:10.1007/BF02184251

Midmore, D.J., 1993. Agronomic modification of resource use and intercrop productivity. Field Crops Res., Intercropping-Bases of Productivity 34, 357–380. doi:10.1016/0378-4290(93)90122-4

Moonen, A.-C., Bàrberi, P., 2008. Functional biodiversity: An agroecosystem approach. Agric. Ecosyst. Environ. 127, 7–21. doi:10.1016/j.agee.2008.02.013

Morgan, J. a. W., Bending, G.D., White, P.J., 2005. Biological costs and benefits to plant–microbe interactions in the rhizosphere. J. Exp. Bot. 56, 1729–1739. doi:10.1093/jxb/eri205

Morris, P.F., Bone, E., Tyler, B.M., 1998. Chemotropic and Contact Responses of Phytophthora sojae Hyphae to Soybean Isoflavonoids and Artificial Substrates. Plant Physiol. 117, 1171–1178. doi:10.1104/pp.117.4.1171

Natarajan, M., Willey, R.W., 1986. The effects of water stress on yield advantages of intercropping systems. Field Crops Res. 13, 117–131. doi:10.1016/0378-4290(86)90015-8

Neumann, G., Römheld, V., 1999. Root excretion of carboxylic acids and protons in phosphorus-deficient plants. Plant Soil 211, 121–130. doi:10.1023/A:1004380832118

Nguyen, C., 2003. Rhizodeposition of organic C by plants: mechanisms and controls. Agron.-Sci. Prod. Végétales Environ. 23, 375–396.

Ortas, I., 2012. The effect of mycorrhizal fungal inoculation on plant yield, nutrient uptake and inoculation effectiveness under long-term field conditions. Field Crops Res. 125, 35–48. doi:10.1016/j.fcr.2011.08.005

Otani, T., Ae, N., Tanaka, H., 1996. Phosphorus (P) Uptake mechanisms of crops grown in soils with low P status: II. Significance of organic acids in root exudates of pigeonpea. Soil Sci. Plant Nutr. 42, 553–560. doi:10.1080/00380768.1996.10416324

Parsons, R., Stanforth, A., Raven, J.A., Sprent, J.I., 1993. Nodule growth and activity may be regulated by a feedback mechanism involving phloem nitrogen*. Plant Cell Environ. 16, 125–136. doi:10.1111/j.1365-3040.1993.tb00854.x

Pelzer, E., Bazot, M., Makowski, D., Corre-Hellou, G., Naudin, C., Al Rifaï, M., Baranger, E., Bedoussac, L., Biarnès, V., Boucheny, P., Carrouée, B., Dorvillez, D., Foissy, D., Gaillard, B., Guichard, L., Mansard, M.-C., Omon, B., Prieur, L., Yvergniaux, M., Justes, E., Jeuffroy, M.-H., 2012. Pea–wheat intercrops in low-input conditions combine high economic performances and low environmental impacts. Eur. J. Agron. 40, 39–53. doi:10.1016/j.eja.2012.01.010

Philippot, L., Raaijmakers, J.M., Lemanceau, P., van der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev. Microbiol. 11, 789–799. doi:10.1038/nrmicro3109

Pivato, B., Mazurier, S., Lemanceau, P., Siblot, S., Berta, G., Mougel, C., Van Tuinen, D., 2007. Medicago species affect the community composition of arbuscular mycorrhizal fungi associated with roots. New Phytol. 176, 197–210. doi:10.1111/j.1469-8137.2007.02151.x

Qiang, C., Peng, H., Gaobao, H., 2004. Effect of intercropping on soil microbial and enzyme activity in the rhizosphere. Acta Prataculturae Sin. 14, 105–110.

Ren, L., Lou, Y., Zhang, N., Zhu, X., Hao, W., Sun, S., Shen, Q., Xu, G., 2013. Role of arbuscular mycorrhizal network in carbon and phosphorus transfer between plants. Biol. Fertil. Soils 49, 3–11. doi:10.1007/s00374-012-0689-y

Requena, N., Jimenez, I., Toro, M., Barea, J.M., 1997. Interactions between plant-growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and Rhizobium spp. in the rhizosphere of

Anthyllis cytisoides, a model legume for revegetation in mediterranean semi-arid ecosystems. New Phytol. 136, 667–677.
Rillig, M.C., Mardatin, N.F., Leifheit, E.F., Antunes, P.M., 2010. Mycelium of arbuscular mycorrhizal fungi increases soil water repellency and is sufficient to maintain water-stable soil aggregates. Soil Biol. Biochem. 42, 1189–1191. doi:10.1016/j.soilbio.2010.03.027
Rillig, M.C., Wright, S.F., Eviner, V.T., 2002. The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant Soil 238, 325–333.
Schachtman, D.P., Reid, R.J., Ayling, S.M., 1998. Phosphorus Uptake by Plants: From Soil to Cell. Plant Physiol. 116, 447–453. doi:10.1104/pp.116.2.447
Schelud'ko, A.V., Makrushin, K.V., Tugarova, A.V., Krestinenko, V.A., Panasenko, V.I., Antonyuk, L.P., Katsy, E.I., 2009. Changes in motility of the rhizobacterium Azospirillum brasilense in the presence of plant lectins. Microbiol. Res. 164, 149–156. doi:10.1016/j.micres.2006.11.008
Scheublin, T.R., Ridgway, K.P., Young, J.P.W., Heijden, M.G.A. van der, 2004. Nonlegumes, Legumes, and Root Nodules Harbor Different Arbuscular Mycorrhizal Fungal Communities. Appl. Environ. Microbiol. 70, 6240–6246. doi:10.1128/AEM.70.10.6240-6246.2004
Schroth, G., 1998. A review of belowground interactions in agroforestry, focussing on mechanisms and management options. Agrofor. Syst. 43, 5–34.
Schulze, J., 2004. How are nitrogen fixation rates regulated in legumes? J. Plant Nutr. Soil Sci. 167, 125–137. doi:10.1002/jpln.200320358
Semere, T., Froud-Williams, R.J., 2001. The effect of pea cultivar and water stress on root and shoot competition between vegetative plants of maize and pea. J. Appl. Ecol. 38, 137–145. doi:10.1046/j.1365-2664.2001.00570.x
Siqueira, J.O., Safir, G.R., Nair, M.G., 1991. Stimulation of vesicular-arbuscular mycorrhiza formation and growth of white clover by flavonoid compounds. New Phytol. 118, 87–93. doi:10.1111/j.1469-8137.1991.tb00568.x
Smith, R.G., 2015. A succession-energy framework for reducing non-target impacts of annual crop production. Agric. Syst. 133, 14–21. doi:10.1016/j.agsy.2014.10.006
Snapp, S.S., Mafongoya, P.L., Waddington, S., 1998. Organic matter technologies for integrated nutrient management in smallholder cropping systems of southern Africa. Agric. Ecosyst. Environ. 71, 185–200. doi:10.1016/S0167-8809(98)00140-6
Song, Y.N., Zhang, F.S., Marschner, P., Fan, F.L., Gao, H.M., Bao, X.G., Sun, J.H., Li, L., 2006. Effect of intercropping on crop yield and chemical and microbiological properties in rhizosphere of wheat (Triticum aestivum L.), maize (Zea mays L.), and faba bean (Vicia faba L.). Biol. Fertil. Soils 43, 565–574. doi:10.1007/s00374-006-0139-9
Spehn, E.M., Joshi, J., Schmid, B., Alphei, J., Körner, C., 2000. Plant diversity effects on soil heterotrophic activity in experimental grassland ecosystems. Plant Soil 224, 217–230. doi:10.1023/A:1004891807664
Stachowicz, J.J., 2001. Mutualism, Facilitation, and the Structure of Ecological Communities Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. BioScience 51, 235–246. doi:10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2
Stephan, A., Meyer, A.H., Schmid, B., 2000. Plant diversity affects culturable soil bacteria in experimental grassland communities. J. Ecol. 88, 988–998. doi:10.1046/j.1365-2745.2000.00510.x
Tang, C., Drevon, J.J., Jaillard, B., Souche, G., Hinsinger, P., 2004. Proton release of two genotypes of bean (Phaseolus vulgaris L.) as affected by N nutrition and P deficiency. Plant Soil 260, 59–68. doi:10.1023/B:PLSO.0000030174.09138.76
Tang, X., Bernard, L., Brauman, A., Daufresne, T., Deleporte, P., Desclaux, D., Souche, G., Placella, S.A., Hinsinger, P., 2014. Increase in microbial biomass and phosphorus availability in the rhizosphere of intercropped cereal and legumes under field conditions. Soil Biol. Biochem. 75, 86–93. doi:10.1016/j.soilbio.2014.04.001
Teplitski, M., Robinson, J.B., Bauer, W.D., 2000. Plants Secrete Substances That Mimic Bacterial N-Acyl Homoserine Lactone Signal Activities and Affect Population Density-Dependent Behaviors in Associated Bacteria. Mol. Plant. Microbe Interact. 13, 637–648. doi:10.1094/MPMI.2000.13.6.637

Tian, C., Li, X., Tang, C., Rengel, Z., Feng, G., Zhang, F., 2002. Improved tolerance of maize plants to salt stress by arbuscular mycorrhiza is related to higher accumulation of soluble sugars in roots. Mycorrhiza 12, 185–190. doi:10.1007/s00572-002-0170-0

Trenbath, B.R., 1993. Intercropping for the management of pests and diseases. Field Crops Res., Intercropping-Bases of Productivity 34, 381–405. doi:10.1016/0378-4290(93)90123-5

Vacheron, J., Desbrosses, G., Bouffaud, M.-L., Touraine, B., Moënne-Loccoz, Y., Muller, D., Legendre, L., Wisniewski-Dyé, F., Prigent-Combaret, C., 2013. Plant growth-promoting rhizobacteria and root system functioning. Front. Plant Sci. 4. doi:10.3389/fpls.2013.00356

Vacheron, J., Renoud, S., Muller, D., Babalola, O.O., Prigent-Combaret, C., 2015. Alleviation of Abiotic and Biotic Stresses in Plants by Azospirillum, in: Cassán, F.D., Okon, Y., Creus, C.M. (Eds.), Handbook for Azospirillum. Springer International Publishing, pp. 333–365.

Valantin-Morison, M., David, C., Cadoux, S., Lorin, M., Amossé, C., Basset, A., 2014. Association d'une culture de rente et espèces compagnes permettant la fourniture de services écosystémiques. Agron. Innov.

van der Heijden, M.G., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1988. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Geol Soc Am Bull 100, 912–927.

van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310. doi:10.1111/j.1461-0248.2007.01139.x

van Kessel, C., Singleton, P.W., Hoben, H.J., 1985. Enhanced N-transfer from a soybean to maize by vesicular arbuscular mycorrhizal (VAM) fungi. Plant Physiol. 79, 562–563.

Vance, C.P., 2001. Symbiotic Nitrogen Fixation and Phosphorus Acquisition. Plant Nutrition in a World of Declining Renewable Resources. Plant Physiol. 127, 390–397. doi:10.1104/pp.010331

Vance, C.P., Graham, P.H., Allan, D.L., 2000. Biological Nitrogen Fixation: Phosphorus - A Critical Future Need?, in: Pedrosa, F.O., Hungria, M., Yates, G., Newton, W.E. (Eds.), Nitrogen Fixation: From Molecules to Crop Productivity, Current Plant Science and Biotechnology in Agriculture. Springer Netherlands, pp. 509–514. doi:10.1007/0-306-47615-0_291

Vance, C.P., Uhde-Stone, C., Allan, D.L., 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol. 157, 423–447. doi:10.1046/j.1469-8137.2003.00695.x

Vandenkoornhuyse, P., Husband, R., Daniell, T.J., Watson, I.J., Duck, J.M., Fitter, A.H., Young, J.P.W., 2002. Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. Mol. Ecol. 11, 1555–1564. doi:10.1046/j.1365-294X.2002.01538.x

Vandermeer, J., 1995. The Ecological Basis of Alternative Agriculture. Annu. Rev. Ecol. Syst. 26, 201–224.

Vandermeer, J., 1992. The ecology of intercropping, 1. paperback ed. ed. Cambridge Univ. Press, Cambridge.

Vandermeer, J., Van Noordwijk, M., Anderson, J., Perfecto, I., 1998. Global chane and multi-species agroecosystems: concepts and issues. Agric. Ecosyst. Environ. 67, 1–22.

Vázquez, M.M., César, S., Azcón, R., Barea, J.M., 2000. Interactions between arbuscular mycorrhizal fungi and other microbial inoculants (Azospirillum, Pseudomonas, Trichoderma) and their effects on microbial population and enzyme activities in the rhizosphere of maize plants. Appl. Soil Ecol. 15, 261–272.

Voisin, A.-S., Salon, C., Munier-Jolain, N.G., Ney, B., 2002. Effect of mineral nitrogen on nitrogen nutrition and biomass partitioning between the shoot and roots of pea (Pisum sativum L.). Plant Soil 242, 251–262. doi:10.1023/A:1016214223900

Walker, T.S., Bais, H.P., Grotewold, E., Vivanco, J.M., 2003. Root Exudation and Rhizosphere Biology. Plant Physiol. 132, 44–51. doi:10.1104/pp.102.019661

Wang, D., Marschner, P., Solaiman, Z., Rengel, Z., 2007. Growth, P uptake and rhizosphere properties of intercropped wheat and chickpea in soil amended with iron phosphate or phytate. Soil Biol. Biochem. 39, 249–256. doi:10.1016/j.soilbio.2006.07.013

Wezel, A., Casagrande, M., Celette, F., Vian, J.-F., Ferrer, A., Peigné, J., 2014. Agroecological practices for sustainable agriculture. A review. Agron. Sustain. Dev. 34, 1–20. doi:10.1007/s13593-013-0180-7

Wichern, F., Eberhardt, E., Mayer, J., Joergensen, R.G., Müller, T., 2008. Nitrogen rhizodeposition in agricultural crops: Methods, estimates and future prospects. Soil Biol. Biochem. 40, 30–48. doi:10.1016/j.soilbio.2007.08.010

Wichern, F., Mayer, J., Joergensen, R.G., Müller, T., 2007. Release of C and N from roots of peas and oats and their availability to soil microorganisms. Soil Biol. Biochem. 39, 2829–2839. doi:10.1016/j.soilbio.2007.06.006

Wieland, G., Neumann, R., Backhaus, H., 2001. Variation of Microbial Communities in Soil, Rhizosphere, and Rhizoplane in Response to Crop Species, Soil Type, and Crop Development. Appl. Environ. Microbiol. 67, 5849–5854. doi:10.1128/AEM.67.12.5849-5854.2001

Willey, R.W., 1990. Resource use in intercropping systems. Agric. Water Manag., Irrigation of Sugarcane and Associated Crops 17, 215–231. doi:10.1016/0378-3774(90)90069-B

Willey, R.W., 1979. Intercropping-Its mportance and research needs. Part . Competition and yield advantages. Field Crop Abstr. 32.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84, 2042–2050.

Zegada-Lizarazu, W., Izumi, Y., Iijima, M., 2006. Water Competition of Intercropped Pearl Millet with Cowpea under Drought and Soil Compaction Stresses. Plant Prod. Sci. 9, 123–132. doi:10.1626/pps.9.123

Zhang, F., Li, L., 2003. Using competitive and facilitative interactions in intercropping systems enhances crop productivity and nutrient-use efficiency. Plant Soil 248, 305–312.

Zhang, G., Yang, Z., Dong, S., 2011. Interspecific competitiveness affects the total biomass yield in an alfalfa and corn intercropping system. Field Crops Res. 124, 66–73. doi:10.1016/j.fcr.2011.06.006

Zhou, D., Huang, X.-F., Chaparro, J.M., Badri, D.V., Manter, D.K., Vivanco, J.M., Guo, J., 2015. Root and bacterial secretions regulate the interaction between plants and PGPR leading to distinct plant growth promotion effects. Plant Soil 401, 259–272. doi:10.1007/s11104-015-2743-7

Zhou, W.-J., Wang, K.-R., Zhang, Y.-Z., Yin, L.-C., Li, H.-S., 2006. Phosphorus Transfer and Distribution in a Soybean-Citrus Intercropping System1 1Project supported by the Knowledge Innovation Programme of the Chinese Academy of Sciences (No. KZCX2-407). Pedosphere 16, 435–443. doi:10.1016/S1002-0160(06)60073-8