



Increase in microbial biomass and phosphorus availability in the rhizosphere of intercropped cereal and legumes under field conditions



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ABSTRACT

Facilitation of plant growth and phosphorus (P) acquisition has recently been reported in cereal–legume intercropping systems. The aim of this study was to test the hypothesis that intercropping could promote P cycling, through microbial biomass P (MBP) changes, in a field trial in a Mediterranean climate. Changes in microbial biomass carbon (MBC), MBP, and inorganic P availability in the rhizosphere of intercropped species were thus investigated in durum wheat/chickpea and durum wheat/lentil intercrops and compared to the bulk soils as well as the rhizosphere of each species grown alone. When expressed relative to the bulk soil, MBC increased in the rhizosphere only for the intercropped plants, irrespective of species. Relative to MBC in the rhizosphere of sole crops, MBC increased in the rhizosphere of the two legume species when intercropped with durum wheat, while no such effect was found for durum wheat. We were unable to detect an increase in P availability in the rhizosphere as a response to intercropping in any of the three crop species, but there was a systematic increase in available P in the rhizosphere relative to the corresponding bulk soil. Fairly similar patterns were observed for MBP as for MBC, except within the rhizosphere of durum wheat when intercropped with chickpea: relative to the bulk soil, MBP increased in the rhizosphere of both lentil and chickpea when intercropped with durum wheat as well as in the rhizosphere of durum wheat when intercropped with chickpea. The differences in microbial biomass changes for a given cereal (durum wheat) when intercropped with two different legumes, suggest that plants have strong species-specific influences on each other as well as on the soil environment. The molar ratios of MBC to MBP (MM C:P) did not vary significantly except for the rhizosphere of durum wheat intercropped with chickpea, which was fairly low (16:1), about half the values found in the other treatments (26–40:1). These MM C:P values were lower than those generally reported in soils (38–60:1), verifying the hypothesis that microbes can increase storage of soil P in their biomass, creating stocks of microbial P in the soil when P availability is high. In this Mediterranean climate where surface soils undergo frequent drying–rewetting, known for liberation of microbial biomass, MBP could be an important factor influencing P availability. Together, our data demonstrate the importance of intercropping to soil P cycling and highlight the need to examine the rhizosphere of each intercropped species to truly understand how the soil P resource is shared in such agroecosystems.

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1. Introduction

Enhanced resource use efficiency has been shown in intercropping systems, which can be defined as two or more species growing simultaneously in the same field, especially in low-input agroecosystems (Trenbeith, 1975; Willey, 1979; Malézieux et al.,

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2009). This positive effect of species diversity in agroecosystems occurs through two main processes: complementarity and facilitation (Fridley, 2001; Hinsinger et al., 2011a). Complementarity can be defined as a decrease in competition through resource partitioning between the intercropped species. It occurs when the species use a given resource differently either in time, space or form (Fridley, 2001). Facilitation represents positive interactions by which one species enhances the growth or survival of another through direct or indirect mechanisms modifying the biotic or abiotic environment of the intercropped species, ultimately resulting in improved resource availability (Callaway, 2007). This occurs when one species increases the availability of a nutrient such as P in the rhizosphere of the intercropped plant species (Li et al., 2007; Hinsinger et al., 2011a).

Improved acquisition of P has been reported in the context of cereal–legume intercrops. However, most of the former studies have been conducted in pots (Li et al., 2004, 2007; Cu et al., 2005). The underlying processes of complementarity and facilitation involved in the rhizosphere of the intercrops have been reviewed by Hinsinger et al. (2011a). In addition to the root-induced direct changes of P availability in the rhizosphere via the exudation of P-mobilizing compounds by roots, facilitation can also occur as a consequence of microbially mediated processes, as a result of a shift in the microbial biomass, activity or community structure. Most former investigations considered the whole (fungi and bacteria) rhizosphere microbial community (Wang et al., 2007) or functional groups mostly linked to the nitrogen (N) cycle (Song et al., 2007; Fan et al., 2011), and to a lesser extent enzymatic activities linked to the P cycle (Li et al., 2009). In soils, microorganisms hold an important role in the mobilization of poorly available P and subsequent increase in the amount of P available for plant acquisition, either via the solubilization of inorganic P pools or the enzymatic hydrolysis of organic P pools. Microorganisms however require P for their own growth. The soil microbial biomass therefore acts as both a source and a sink for nutrients such as P, which become available through the turnover of soil microorganisms, e.g. via predation by soil microfauna (Cole et al., 1977; Irshad et al., 2012).

Considering the P dynamics and cycling in soil, the amount of P held in microorganisms, i.e. microbial biomass P (MBP), may thus constitute a significant component of the total soil P (Xu et al., 2013). This pool can be a substantial source of available P for plant growth, especially in organic-rich soils as occur in pasture and forest ecosystems (Oberson and Joner, 2005; Achat et al., 2010). The MBP is expected to be smaller in arable land than in pasture and forest soils, as there is less organic matter (Oehl et al., 2001; Oberson and Joner, 2005; Richardson et al., 2011; Xu et al., 2013). The concentration and forms of microbial P can change with the composition of the microbial community (Bünemann et al., 2011), the growth stage of microorganisms (Elser et al., 2003), and environmental conditions (Makino and Cotner, 2004; Cotner et al., 2006). According to Alexander (1977), the dominant forms of microbial P in bacteria and fungi are RNA (30–50%), acid-soluble inorganic and organic P (including sugar and nucleotide esters and various phosphorylated coenzymes and polyphosphates, 15–20%), phospholipids (10%), DNA (5–10%) and small amounts of inositol phosphates. The proportion of RNA-P in microbial cells can increase with the growth rate under low P conditions (Elser et al., 2003); in addition bacteria can accumulate excess P as polyphosphates under high P conditions, which can be used as P reserves under P-limiting conditions (Grant, 1979; Kulaev and Kulakovskaya, 2000). At the global scale, the soil microbial biomass C:N:P stoichiometry is rather well-constrained, indicating a fixed ratio of the relative demand of soil microbes for C, N and P (Cleveland and Liptzin, 2007; Xu et al., 2013). However, such large-scale stoichiometry patterns mask the considerable variability for

individual phylogenetic groups within soil microbial community that occur in various biomes. Significant variation in the C:N:P ratios of soil microbes across land use and habitat types has been observed, especially for C:P and N:P, while C:N was much less variable (Cleveland and Liptzin, 2007; Hartman and Richardson, 2013). Importantly, both biomass stoichiometry and the degree of homeostatic response to nutrient availability appear to vary among different bacteria, and with the degree of nutrient limitation. Scott et al. (2012) studied isolated heterotrophic bacteria across an ecologically-relevant range of C:P ratios and found that bacterial stoichiometry was very flexible under P-sufficient and P-deficient treatments. At community scale, bacteria may exhibit flexible stoichiometry as a result of species sorting, lower C:P ratio in the environment selecting for bacteria with lower biomass C:P ratio (Danger et al., 2008). Strong or weak homeostasis in a bacterial community may have important implications for P cycling. Considering the species-specific effect of plants on rhizosphere microbial community in intercropping system, it is meaningful to investigate the microbial biomass C:P ratios in the rhizosphere of intercrops, compared to those of each of the two crop species when grown alone.

In our study, two cereal/legume intercropping systems, durum wheat/chickpea and durum wheat/lentil, were investigated in a field experiment. Firstly, we evaluated the effect of intercropping on soil P availability and microbial biomass. We hypothesized that intercropping leads to an increase in MBC and MBP in the rhizosphere due to a higher diversity of rhizodeposits. Secondly, we tested if intercropping altered microbial C:P ratios to reflect growth versus storage of P in the microbial community.

2. Materials and methods

2.1. Site description, management and field plot design

The field experiment was conducted at Manguio INRA experimental station in Southern France (35°9'03"E, 43°7'14"N) in 2009–2010. The regional climate is typical Mediterranean, with surface soils regularly undergoing drying–rewetting cycles from the irregular distribution of rainfall. The annual average rainfall at this site during the growing season, from September to June, over the last 50 years was 704 mm; while it amounted to 538 mm in 2009–2010, with a much wetter February and a much drier March, April and June, resulting in 4 cycles of drought prior to sampling (drought considered 20 days with under 2 mm cumulative rainfall). The soil was a calcareous cambisol with a sandy clay loam texture (clay 194 g kg⁻¹, fine silt 273 g kg⁻¹, coarse silt 217 g kg⁻¹, fine sand 177 g kg⁻¹ and coarse sand 140 g kg⁻¹), which had developed on an alluvial calcareous parent material, typical of the Mediterranean plains South-East of Montpellier. It received large P-fertilizer rates for 25 years, until this part of the experimental station was converted to organic farming one year before the experiment was sown. Since then, it did not receive any fertilizer. The soil exhibited a rather high content of available P (42 mg kg⁻¹ Olsen P), presumably non-limiting for plant growth. Additional soil properties were as follows: total CaCO₃ 51 g kg⁻¹, pH 8.29, CEC 21.1 cmol_c kg⁻¹, organic C 9.3 g kg⁻¹, total N 0.89 g kg⁻¹, total P 661 mg kg⁻¹, soil molar ratios of C:N 12.2, C:P 36.4, N:P 3.0.

Two cereal–legume intercrops and each sole crop were tested using a randomized block design, with four replicates and plot sizes of 6 m × 10 m. When grown alone (sole crops), durum wheat (*Triticum turgidum durum* L. cv. LA1823) was sown at 250 seeds m⁻², while chickpea (*Cicer arietinum* L. cv. Daisy Elmo) and lentil (*Lens culinaris* L. cv. Anicia) were sown at 35 seeds m⁻². We used a substitutive design with each of the two crops sown at half densities when intercropped. The crops were sown in November 2009

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