



Research paper

Species interactions enhance root allocation, microbial diversity and P acquisition in intercropped wheat and soybean under P deficiency



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ABSTRACT

Belowground interactions in grain legume-cereal intercrops may improve resource acquisition and adaptation to environmental constraints such as phosphorus (P) deficiency. To advance the knowledge of belowground facilitative mechanisms involved in P-deficiency tolerance (root allocation, biochemical and microbial responses), soybean (*Glycine max*) and wheat (*Triticum aestivum*) were grown as monocrops and intercrops under P-deficiency and P-sufficiency conditions in soil-filled rhizoboxes. The hypothesis was that intercropping stimulates root microbial diversity, root biomass allocation and P-hydrolyzing acid phosphatases (APase) activity in roots under P-deficient conditions. Total root dry weight (RDW), length, and surface area significantly increased in P-deficient intercropped wheat and soybean. Greater root allocation to deeper soil layers was evident for P-deficient intercropped wheat. Shallow roots of intercropped wheat exhibited highly stimulated APase activity under P-deficient conditions while shallow roots of monocropped soybean exhibited higher APase activity in comparison to deeper roots, irrespective of P treatment. Root fungal diversity was significantly ($p < 0.05$) higher in intercropped wheat, and was significantly correlated with RDW, root APase activity, shoot P, and soil available P ($\rho = 0.24$, $p = 0.01$). Root bacterial diversity was higher in both intercrops, and was significantly correlated with RDW and shoot N concentration. The observed shifts in root microbial diversity, root biomass allocation and APase activity provide explanatory mechanisms of relationships between rhizosphere heterogeneity and pathways for increased P acquisition in diversified crops. Advanced belowground metabolomics on root microbial communities are required to reveal the beneficial effect of root microorganisms in associations of different crop species.

1. Introduction

Improving growth and yield performance of staple food crops such as legumes and cereals are major concerns for current and future agriculture, especially in stressed environments where increased frequency of abiotic constraints such as drought (Link et al., 1999; Wang et al., 2003), salinity (Munns and Tester, 2008), and low soil fertility (Graham and Vance, 2003) cause drastic yield losses. Low soil nutrient availability, notably phosphorus (P), is among the most important abiotic constraints for plant growth, especially for legumes whose sensitivity to P-deficiency has been attributed to higher P requirements during the symbiotic N₂ fixation process (Vance, 2001; Graham and Vance, 2003; Schulze and Drevon, 2005; Bargaz et al., 2011; Isaac et al., 2012).

While nutrients removed with harvested crops ultimately need to be

replaced by recirculation or new inputs to avoid soil nutrient depletion, efficient crop nutrient acquisition is a key function for developing sustainable cropping systems that prevent nutrient losses and are able to maintain high productivity with moderate external inputs. The practice of intercropping legumes with cereals is gaining interest worldwide due to an increasing desire for optimizing use of mineral resources (Fujita et al. 1992; Hauggaard-Nielsen and Jensen, 2005; Long et al., 2014; Brooker et al., 2015). Intercropping may mitigate stressful environmental conditions and increase the availability of deficient soil resources (Li et al., 2003; Betencourt et al., 2012; Pang et al., 2013; Isaac et al., 2014; Bargaz et al., 2015; Latati et al., 2016a). Furthermore, intercropping has enhanced transfer of symbiotically-fixed nitrogen (N) from intercropped legumes to intercropped cereals (Xiao et al., 2004; Isaac et al., 2012), increased soil fertility (Wang et al., 2015), increased yield stability (Nasielski et al., 2015), and decreased

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the prevalence of damage by pests, disease, and weeds (Jensen, 1996; Trenbath, 1993; De Vallavieille-Pope, 2004; Corre-Hellou and Crozat, 2005; Li et al., 2007; Hauggaard-Nielsen et al., 2009).

Legume-cereal intercrops confer niche differentiation for more efficient exploitation of limiting resources and optimize rhizosphere biochemical heterogeneity (Corak et al., 1987; Li et al., 2001, 2007; Knudsen et al., 2004; Banik et al., 2006; Pang et al., 2013). Of note, the stimulation of legume nodulation and beneficial rooting distribution enhances acquisition of deficient resources, notably P and water, providing an advantage to both intercropped-species (Li et al., 2007; Betencourt et al., 2012; Pang et al., 2013; Bargaz et al., 2016). Moreover, it has been demonstrated that enhanced nodulation in intercropping also coincided with a higher root biomass and distribution in the soil and that has led to a significant correlation between biomass of shoot and nodules (Latati et al., 2014, 2016a, 2016b; Bargaz et al., 2016). Faster root growth has been reported in legume-cereal intercrops, associated with higher P uptake, though largely in the cereal rather than the legume (Hauggaard-Nielsen et al., 2001; Li et al., 2006). Root length and distribution is correlated to shoot biomass accumulation in a maize – faba bean or – chickpea intercrop (Xia et al., 2013). Moreover, differential contribution from the above- and below-ground parameters to intercropping system performance was observed by Zhang et al. (2010).

For, specifically, plant P nutrition, rhizospheric interspecific facilitation has been found to increase availability and acquisition of P in several legume-based intercropping systems: wheat-lupine (Horst and Waschki, 1987), sorghum-pigeon pea (Ae et al., 1990), wheat-chickpea (Li et al., 2003), maize-peanut (El Dessougi et al., 2003), wheat-chickpea (Li et al., 2004; Betencourt et al., 2012), maize-chickpea (Li et al., 2004), maize-faba bean (Li et al., 2003, 2004, 2007), barley-pea (Hauggaard-Nielsen et al., 2009), and maize-cowpea (Latati et al., 2014). The main physiological mechanisms driving this P use efficiency under P-deficiency (Li et al., 2003, 2004; Veneklaas et al., 2003) are most likely due to the stimulation of rhizodeposits including carboxylates exudation, protons, and the activity of P-hydrolyzing enzymes, such as acid phosphatases (APase). Contribution of APase activity to the facilitation of P uptake in intercropping was reported in studies on maize-chickpea (Li et al., 2004), maize-peanut (Inal et al., 2007), and barley-peanut (Inal and Gunes, 2008) in which the intercropped legume exhibited higher APase activity in roots and rhizosphere soils compared to the intercropped cereal. Induced root and soil APase activity in intercropping (compared to monocropping) has been attributed to an enhanced demand for P to support both intercropped-species (Inal et al., 2007).

Other plant-root exudates, such as organic acids, which are potentially implicated in P solubilization, may also be considered as key drivers in microbial recruitment and proliferation within the different rhizosphere layers e.g. ecto-rhizosphere, rhizoplane, and endo-rhizosphere (Hunter et al., 2014). This also includes root-associated and/or endophytic microbial populations that are responsible for a substantial pool of solubilized inorganic nutrients (e.g. P, Mg, Ca, Fe, etc.) in mixed cropping systems (Loper and Buyer, 1991; Dakora et al., 2003; Hunter et al., 2014). Legume-cereal intercrops show a number of rhizosphere-induced modifications including rhizosphere microbial communities (Morgan et al., 2005; Song et al., 2007; Sun et al., 2009) as well as a significant increase in microbial biomass P and C in the rhizosphere of intercropped legumes (Tang et al., 2014). Despite clear evidence of improved growth and yield in legume-cereal intercropping systems, further research on the highly intricate plant-soil-microbe continuum is needed, particularly under low soil nutrient availability. We hypothesize that crop diversification by grain legume-cereal intercropping under low P availability will enhance root allocation, root microbial diversity, and APase activity. We also hypothesize that these biophysical traits will be highly stimulated in intercrops resulting in improved P acquisition and growth. The specific objectives of this study were to (1) determine the effects of crop diversity on root allocation and

distribution (in space) as an adaptive mechanism in response to P-deficiency (2) assess mono- and inter-cropping effects on root microbial diversity and (3) track variations in APase activity under different cropping strategies. To do this, we measured root functional traits, root microbial communities, root APase activity, and aboveground performance (growth) in wheat and soybean grown as mono- and intercrops under contrasting P availability in soil-filled rhizoboxes.

2. Material and methods

2.1. Soil, plant material and experimental design

A greenhouse experiment was conducted at the University of Toronto Scarborough, Canada, during spring and summer 2014 under natural daylight conditions (16 h photoperiod) supplemented with 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. Day/night temperatures were 25/20 °C, and the relative humidity was kept at approximately 65%. Disease-free seeds of soybean (*Glycine max* L.cv Pioneer P90Y90) and spring wheat (*Triticum aestivum* L. cv Sable) were germinated for ten days in sterilized peat. Seedlings were transplanted into plexiglass rhizoboxes measuring 40 × 30 × 3.5 cm, and constructed with a removable and re-sealable plexiglass front (Bargaz et al., 2015). Rhizoboxes facilitated access to the rhizosphere soil and permitted a non-destructive recovery of roots and nodules. Rhizoboxes were filled with 6 kg sieved (2-mm) and mixed air-dried soil and sand (30 volume-% soil, 70 volume-% sand). The soil used was collected from the top 20 cm in the agroforestry research station at the University of Guelph (Guelph, Ontario, Canada). Soils at the Guelph site are classified as Gray Brown Luvisols with a sandy-loam soil texture (Order: Alfisols, Group: Typic Hapludalf) (Oelbermann and Voroney, 2007). They are characterized as neutral pH, with low total nitrogen (0.7 g kg⁻¹) and available P (3 mg kg⁻¹) concentration. Pooled analysis for soil inorganic N (soil nitrate: 15.76 ± 1.86 mg NO₃⁻ kg⁻¹ and soil ammonium: 9.28 ± 6.10 mg NH₄⁺ kg⁻¹) indicate a moderately N deficient soil.

The experimental design was comprised of two factors: (1) cropping treatment (monocropped soybean (S), monocropped wheat (W), and intercropped S and W) and (2) P level (sufficient and deficient). The experiment was performed in a replacement design where the relative plant density remains constant across monocropping and intercropping treatments, a common approach to assess legume-cereal intercropping interactions (Hauggaard-Nielsen et al., 2009). The planting density was four plants per rhizobox, with two plants of each species per rhizobox in the intercropping treatments (4W or 4S for monocropped and 2W + 2S for intercropped) with the abbreviations S for monocropped soybean; W for monocropped wheat; SW-s for intercropped soybean; and SW-w for intercropped wheat. The entire experiment was replicated in three blocks with three rhizoboxes per treatment. Plants were grown at approximately 80% field capacity using a nutrient solution (Bargaz et al., 2011, 2012) with either 125 or 25 $\mu\text{mol P}$ per rhizobox per week defined as sufficient and deficient P treatments, respectively. Urea was added at a concentration of 1 mmol (equivalent to 60 mg) per rhizobox in the nutrient solution during the initial 15 days after transplantation (DAT). After this, plants were grown with N-free nutrient solution, *i.e.* totally dependent on both soil N and symbiotic N₂ fixation (soybean).

2.2. Measurement of above-and below-ground plant growth performances

At 45 DAT, plants were collected and separated into shoots and roots (nodulated roots for soybean) at the cotyledon node. The rhizosphere soil was obtained by carefully separating roots from the loosely adhering soil, which was then sieved (2 mm) prior to measurements of APase activity and Olsen P concentration. The roots and nodules were carefully washed with distilled water at 4 °C. Fresh root fractions were sampled and immediately frozen at -20 °C before they were analyzed for APase activity and microbial community.

Root surface (cm²) and length (cm) were measured using the automated image analysis software WinRhizo 2005b (Regent Instruments).

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