Plant Soil
DOI 10.1007/s11104-012-1236-1

REGULAR ARTICLE

Soil pH is the main factor influencing growth and rhizosphere properties of wheat following different pre-crops

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Received: 12 November 2011 / Accepted: 27 March 2012

Abstract
Background Phosphorus utilization efficiency is very low in soil due to its low solubility and mobility. Legumes have been shown to increase P uptake of the following wheat, but the underlying mechanisms of this effect are unclear.
Materials and methods Using three soils with low P availability differing in pH and therefore predominant P form: Mount Bold (pH 4.8), Monarto (pH 7.5) and Langhorne Creek pH 8.8), a rotation of faba bean, white lupin and wheat and unplanted soil in phase 1 and wheat in phase 2 was grown. To distinguish between the pre-crop effect and the residue effect, the residues from the pre-crops in phase 1 were either returned to the pre-crop soil or added to the previously unplanted soil. In the rhizosphere of wheat, P fractions were determined and the community composition of bacteria, fungi, P mobilizers (ALP gene), ammonia-oxidizing bacteria (AOB) and archaea (AOA) were analyzed by polymerase chain reaction (PCR) – denaturing gradient gel electrophoresis (DGGE).
Results There were no differences in wheat root and shoot biomass among treatments in the acidic Mount Bold soil, but in both the alkaline Langhorne Creek and neutral Monarto soils, wheat shoot biomass was highest in wheat and white lupin pre-crop soils. The alkaline Langhorne Creek soil had the highest concentrations of HCl P, whereas NaOH I Pi, NaOH I Po, NaOH II Pi, residual P and total P were highest in the acidic Mount Bold soil. In the soil with residues, the presence of plants in phase 1 of the rotation increased the concentrations of labile P pools and the NaOH extractable P pools in the rhizosphere of wheat compared to wheat grown in the previously unplanted soil, with the increase occurring in both inorganic and organic P fractions. As the amount of residues added in the soil was only 1 $g kg^{-1}$, the effect of the residues alone on soil P pools was relatively small. The community composition of all microbial groups investigated differed among soils and within one soil by the pre-crop. Among the pre-crops, white lupin had a negative effect on AMF colonization although resin P concentrations were not higher than in the other pre-crop treatments.
Conclusions Soil P pools and microbial community composition were predominantly affected by soil pH and within a given soil by the pre-crop treatment whereas the residue effect was small. The finding that

Responsible Editor: Tim Simon George.

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Published online: 18 April 2012

in two of the soils the presence of plants in phase 1 of the rotation increased P uptake by 6 week-old wheat but also increased the concentrations of labile P pools and the NaOH extractable P pools in the rhizosphere of wheat suggests that pre-crops may enhance P uptake by wheat also in the later stages of growth.

Keywords Microbial community · Nitrification · P fractions · pH · Pre-crop · Residues · Rhizosphere · Rotation

Introduction

Phosphorus is the second most limiting nutrient for crops and often addition of P fertilizer is essential to maintain crop yields. However, the amount of P fertilizer which is taken up in the year of application is relatively low, i.e. only 10-15 %, thus leading to P accumulation in soil and potentially environmental pollution (Borda et al. 2011). Additionally, P fertilizers are produced from phosphate rock which is a non-renewable limited resource (IFA 2010). Thus, it is important to improve P management by enhancing soil P availability and utilization efficiency. Phosphorus acquisition efficiency is enhanced, for example by increasing root length, density, surface area (Li et al. 2009; Shimizu et al. 2004) or changing root distribution and root architecture (Lynch 1995; Lynch and Brown 2001). In the rhizosphere, exudates from roots and microbes enhance P mobilization, including organic anions (Wang et al. 2007), phytase (Richardson et al. 2000; Starnes et al. 2008) and phosphatase (George et al. 2008; Li et al. 2004; Sen and Mukherji 2004). In rotations, legumes are used to increase N availability to the following cereals. Additionally, some legumes (e.g. faba bean, white lupin, pigeon pea) have a higher ability than cereals to mobilize poorly soluble P (Ae et al. 1990; Li et al. 2003). Previous studies have shown higher P uptake of cereals following faba bean and white lupin (Nuruzzaman et al. 2005), or intercropped with pigeon pea (Ae et al. 1990), white lupin (Cu et al. 2005), chickpea (Li et al. 2003, 2004) and faba bean (Hinsinger et al. 2011; Li et al. 2007). There are several hypotheses or potential mechanisms explaining the positive effect of legumes on P uptake by cereals, including (1) exudation of carboxylates by legumes (Wang et al. 2007) which compete with phosphate for binding sites in the soil, (2) acidification (Zhu et al. 2005) or alkalinization (Bagayoko et al. 2000; Rose et al. 2010) which increases the solubility of P salts, (3) different P pools used by legumes and cereals, or legumes increasing the concentration of the labile P pools, and (4) P release from residues (Ha et al. 2007) or soil P mobilization by carboxylates produced during decomposition (Iyamuremye et al. 1996). Of these mechanisms, the first two have been studied extensively whereas less is known about the third and fourth mechanisms. Further, it is not clear how important the effect of residues is compared to that of the pre-crop alone.

Soil pH affects the predominant forms of P which, in turn are mobilized by different mechanisms. In acidic soils, Fe and Al phosphates as well as P bound to Fe and Al oxides dominate that can be mobilized by organic anions by chelating metals and ligand exchange, whereas the Ca-bound phosphates dominating in alkaline soils are mainly mobilized by acidification (Hinsinger 2001; Lindsay 1979). In a previous study with the same soils as used here, faba bean, white lupin and wheat were grown in monoculture or in mixed culture of wheat with legumes (Wang et al. 2011, in press), Plant growth and rhizosphere microbial community composition and soil P pools were predominately affected by soil type whereas the cropping system (monoculture versus mixed culture) had little effect. In that study, wheat and legumes depleted less labile inorganic P whereas less labile organic P only accumulated in the rhizosphere of the legumes (for a definition of less labile P, see below in the Materials and Methods section).

The aim of this rotation study was to assess the relative importance of soil pH, residues and pre-crops on the growth and rhizosphere properties of the following wheat. In a glasshouse study, three soils with low available P concentration differing in pH (4.8, 7.5 and 8.8) were used. In phase 1 of the rotation, faba bean, white lupin and wheat were grown, and unplanted soil was kept under the same conditions. Then in phase 2, wheat was grown in pre-crop soil mixed with the respective residue or in previously unplanted soil mixed with residues from faba bean, white lupin and wheat or without residues.

Materials and methods

Experimental design

The soils used in this study were collected from three locations in South Australia: Mount Bold (acidic,

Table 1 Properties of the soils

Soil property	Langhorne Creek	Monarto	Mount Bold
Clay %	22	8	20
Silt %	6	10	27
Sand %	74	82	53
Texture	Sandy clay loam	Loamy sand	Sandy loam
Organic C (g kg^{-1})	12	13	44
Water holding capacity (%)	16.4	15.8	34.5
pH	8.8	7.5	4.8
Inorganic N (mg kg^{-1})	23	59	33
Available P (mg kg^{-1})	11.3	4.5	3.7
Microbial P (mg kg^{-1})	5.0	9.0	17.8
Total P (mg kg^{-1})	180	230	374

38 °11′S and 138 °69′E), Monarto (neutral, 35 °50′S and 139 °60′E), and Langhorne Creek (alkaline, 35 °16′S and 139 °9′E) (Table 1).

For the first phase of the rotation (pre-crop phase), the soils were amended with basal nutrients (g kg^{-1} soil): K_2SO_4 0.17, $MgSO_4$ 0.19, and with micronutrients (mg kg^{-1} soil) FeNaEDTA 0.4, $CuSO_4 \cdot 5H_2O$ 2.0, $MnSO_4 \cdot 4H_2O$ 0.6, $CoCl_2 \cdot 6H_2O$ 0.4, H_3BO_3 0.5, $Na_2MoO_4 \cdot 2H_2O$ 0.5, and $ZnSO_4 \cdot 7H_2O$ 2.2 (Li et al. 2011) and with 10 mg P kg^{-1} as KH_2PO_4 . Nitrogen was added to wheat at 150 mg N kg^{-1} as $(NH_4)_2SO_4$; this N rate was chosen to ensure that N was not limiting wheat growth. The legumes were grown without nitrogen addition and inoculated with the appropriate *Rhizobium* strain: strain WU425 (group G) for white lupin, strain WSM1455 (group F) for faba bean. Pregerminated seeds of white lupin (*Lupinus albus* L. cv. Luxor) (L), faba bean (*Vicia faba* L. cv. Fiesta) (F) and wheat (*Triticum aestivum* L. cv. Krichauff) (W) were planted and later thinned to 2 plants per pot with 4 replicates. Wheat was planted 2 weeks after the legumes because of the more rapid development of wheat. Additionally, there were 16 pots per soil without plants in this phase which received the basal nutrients without P and N. The plants were harvested 8 weeks after sowing of the legumes at which time legumes and wheat were in the early flowering stage. The roots of the pre-crops were carefully removed from the soil which was then air-dried to mimic the conditions in the field in Southern Australia where soils often dry out during the hot and dry summer before the following crop is planted after the onset of the autumn rains.

The root and shoot residues were dried at 40°C, cut to about 2 cm and then mixed into the soil previously cropped with legumes or wheat (pre-crop soil: F+RF, L+RL, W+RW) or the previously unplanted soil (U+RF, U+RL, U+RW) at a rate of 1 g kg^{-1}. The soils were filled into 1 kg pots, adjusted to 70 % WHC and planted with germinated seeds of wheat (*Triticum aestivum* L. cv. Krichauff). Additionally there were 4 pots of previously unplanted soil without residues which were left unplanted (UP no wheat) and 4 pots of previously unplanted soil without residues planted with wheat (UP)(for the treatments see Table 2). No nutrients were added in the second phase of the rotation. The wheat was thinned to 2 plants per pot and grown for 6 weeks.

The soil was maintained at 70 % water holding capacity throughout phases 1 and 2 by adjusting the weight of the pots with water every 1-2 days. Six weeks after planting, the roots of wheat were carefully removed from the soil. After shaking off the loosely

Table 2 Overview of the experimental design and treatment names

Phase 1	Unplanted					Faba bean (FB)	White lupin (L)	Wheat (W)
Residue treatment		None	+ FB	+ L	+W	+ FB	+ WL	+W
Phase 2	Unplanted					Wheat		
Name	UP no plant	UP	UP+RF	UP+RL	UP+RW	F+RF	L+RL	W+RW

adhering soil, the tightly adhering rhizosphere soil was collected with a brush and stored at -20°C for DNA extraction and at 4°C for the other analyses. Storage at 4°C was used because freezing and thawing may induce changes in nutrient availability (Feng et al. 2007).

Soil texture was determined as described by Bowman and Hutka (2002) and the soils classified according to the USDA classification system. The total organic C (TOC) concentration was determined by wet oxidation and titration (Walkley and Black 1934). The water holding capacity was determined after Wilke (2005).

Plant analysis

The shoots and roots were oven-dried at 70°C for 2 days and ground for plant N and P analysis. The N concentration was determined using the Kjeldahl method (Bradstreet 1965) and the N concentration was measured colorimetrically (Bremner 1965). The P concentration was determined after digestion in a mixture of nitric acid and perchloric acid (6:1) (Kuo 1996).

Arbuscular mycorrhizal (AM) colonization

Arbuscular mycorrhizal colonization was assessed only in wheat in phase 2 of the rotation. Subsamples of wheat roots (~0.2 g) were cut to approximately 1 cm length before clearing in KOH 10 % for 3 days at room temperature and then stained as described in Vierheilig et al. (1998). Stained roots were assessed for AM colonization using the gridline intersection method (Brundrett et al. 1996; Giovannetti and Mosse 1980) under a dissecting microscope at 40 X magnification.

Soil pH, ammonium, nitrate and nitrification potential activity (PNA) and microbial biomass

Soil pH was measured using 2 g soil at a 1:5 soil-water ratio in rhizosphere and unplanted soil.

Nitrate and ammonium were extracted from the bulk soil by horizontal shaking with 2 M KCl (1:10) for 1 h and determined by the cadmium reduction method for nitrate (Henrikson and Selmer-Olsen 1970) and with nitroprusside/dichloro-S-triazine for ammonium (Searle 1984). Potential nitrification activity (PNA) was determined by the shaken soil slurry method as described previously (Shen et al. 2008) without potassium chlorate. Chloroform-labile C as a measure of soil microbial biomass carbon was measured by the fumigation-extraction method (Joergensen and Brookes 1990) except 4 g soil and 16 ml 0.5 M K_2SO_4 extractant were used.

Soil DNA extraction and denaturing gradient gel electrophoresis (DGGE) analysis

Soil DNA was extracted from 0.5 g rhizosphere soil using the Ultraclean® Soil DNA Isolation Kit (MOBIO) according to the manufacturer's protocol except for the initial step which was bead beating at 5.5 ms^{-1} for 40 s. The purified DNA was diluted with 50 μl sterilized water.

The PCR was performed with 1 X PCR buffer without $MgCl_2$ (QIAGEN), 2.0 mM $MgCl_2$ (QIAGEN), 0.5 μl dNTP mix (10 mM of each) (QIAGEN), 6 pmol of each primer, 0.2 μl Taq DNA polymerase (5 unit μl^{-1}) (QIAGEN), 1 μl 10 times diluted soil DNA, and water to the final volume of 25 μl. The primers used and thermal profiles are given in Table 3.

Denaturing gradient gel electrophoresis analysis of the PCR products was performed with the DCode Universal Mutation Detection System (Bio-Rad Laboratories). The PCR products of bacteria, fungi, alkaline phosphatase (ALP) genes, nitrogen fixing (nifH) genes, ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) were loaded onto polyacrylamide gels with a denaturing gradient (100 % denaturant contains 42 g urea and 40 ml formamide in 100 ml) as shown in Table 3. Electrophoreses were run at 80 V for 16 h in 1 X TAE. The gels were stained with 0.001 % SYBR Gold (Invitrogen) for 45 min, visualized under blue light, and digitized by the software Quantity One (Bio-Rad Laboratories).

Soil P fractionation

Soil P fractions were determined in phase 2 of the rotation in the rhizosphere of wheat and the unplanted soil based on the method described by Condron and Goh (1989) and Tiessen and Moir (1993) with slight modifications. One g soil was shaken with 15 ml water and an anion exchange (#55164, BDH Chemicals, Poole, England) strip (3 X 2 cm) for 16 h; another aliquot was amended with 1 ml hexanol to extract microbial P (Kouno et al. 1995). A conversion factor of 0.4 was used to calculate microbial biomass P from

Table 3 Primers, PCR conditions and DGGE gradients used for microbial community analysis

Group	Primer pair	Primer sequence	Reference	Temperature profile	DGGE gradient
Bacteria	357f-GC[a]	5'-CGCCCGCCGCG CGCGGCGGGCG GGGCGGGGGCA CGGGGGG-CCTA CGGGAGGCAGC AG-3'	(Muyzer et al. 1993)	94°C, 4 min, and 94°C, 45 s, 55°C, 30 s, 72°C, 1 min, 30 cycles for bacteria or 35 cycles for fungi and 72°C, 8 min for final extension.	35-55 %
	518r	5'-ATTACCGCGGC TGCTGG-3'			
Fungi	ITS1-F-GC	5'-CGCCCGCCGC GCGCGGCGGG CGGGGCGGGG GCACGGGGGG-TCCGTAGGTGA ACCTTGCGG-3'	(Anderson et al. 2003)		10-50 %
	ITS2	5´-GCT GCGTTC TT ATCGATGC-3´			
ALP gene	ALPS-F730	5'-CAGTGGGAC GACCACGAGGT-3'	(Sakurai et al. 2008)	94°C, 4 min, and 94°C, 45 s, 57°C, 30 s, 72°C, 1 min, and 72°C for 35 cycles, 8 min for final extension.	45-70 %
	ALPS-R1101-GC	5'-CGCCCGCCGC GCGCGGCGG GCGGGGCGG GGGCACGGG GGG-GAGGC CGATCGGCA TGTCG-3'			
nifH gene	PolF	5'-TGCGAYCCS AARGCBGACTC-3'	(Poly et al. 2001; Zhang et al. 2008)	94°C, 4 min, and 94°C, 45 s, 55°C, 30 s, 72°C, 1 min, 30 cycles with 2 round (1st round without GC with forward primer and 2ed with GC), and 72°C, 8 min for final extension.	45-65 %
	PolF-GC	5'-CGCCCGCCG CGCGCGGCGG GCGGGGCGGG GGCACGGGGG G-TGCGAYCCS AARGCBGACTC-3'			
	PolR	5'-ATSGCCATCA TYTCRCCGGA-3'			
AOB	amoA-1 F-GC	5'-CGCCCGCCG CGCGCGGCG GGCGGGGCG GGGGCACGG GGGG-GGGG TTTCTACTGG TGGT-3'	(Nicolaisen and Ramsing 2002)	94°C, 4 min, and 94°C, 45 s, 55°C, 30 s, 72°C, 1 min 37 cycles for AOB and AOA, and 72°C, 8 min for final extension.	35-60 %
	amoA-2R	5'-CCCCTCKGS AAAGCCTTC TTC-3'			
AOA	Arch-amoAF	5'- STAATGGTCT GGCTTAGACG-3'	(Francis et al. 2005)		20-45 %
	Arch-amoAR-GC	5'-CGCCCGCCGC GCGCGGCGGGC GGGGCGGGGGC ACGGGGGG-GC GGCCATCCATC TGTATGT-3			

[a] the GC clamp used in this study was same as Muyzer et al. (1993)

the difference between hexanol-labile P and resin P (Kouno et al. 1995). The soil treated with hexanol (after removal of microbial biomass P) was further sequentially extracted with 30 ml of 0.5 M $NaHCO_3$, 0.1 M NaOH, 1 M HCl, 0.1 M NaOH and 15 ml concentrated HCl; the remaining soil was used to determine residual P. The second extraction with NaOH was carried out because Condron and Goh (1989) suggested that substantial amounts of P were released by NaOH after removal of the 1 M HCl soluble P. In all fractions, inorganic P was determined colorimetrically using the method described by Murphy and Riley (1962). Organic P was determined in the 0.5 M $NaHCO_3$, 0.1 M NaOH, 0.1 M NaOH, concentrated HCl fractions by persulfate oxidation. The concentration of organic P was calculated as the difference between total P in the extract treated with persulfate and inorganic P (Tiessen and Moir 1993). Soil total P and residual P were measured after digestion in a mixture of nitric acid and perchloric acid (6:1) (Kuo 1996).

Statistical analysis

Two-way analysis of variance was performed using Genstat (GenStat® for Windows10.0, VSN Int. Ltd, UK, 2005). With a few exceptions (see below for details), the main effects (soil pH and treatment) as well as their interaction was significant at $P \leq 0.05$. The least significant difference in tables and figures refers to the interaction term. Statements in the text about differences among treatments refer to significant differences ($P \leq 0.05$).

Microbial community composition based on the digitized DGGE profiles was analyzed with Primer E software (Primer-E Ltd, Plymouth Marine Laboratory, Plymouth, UK). Non-metric multidimensional (MDS) scaling based on band position and peak height was used to plot the DGGE profiles. Unlike principle component analysis plots, MDS plots do not have axis units or labels. The 2D stress indicates how well the plot represents the variability in the data with a 2D stress <0.2 considered to represent a good reflection of the resemblance matrix (Clarke and Warwick 2001). Significant differences in microbial community composition between treatments were determined by PERMANOVA (Primer-E Ltd, Plymouth Marine Laboratory, Plymouth, UK).

Results

Pre-crops

The shoot and root biomass of the pre-crops was greatest in faba bean and smallest in wheat (Table 4). Total N in the residues was greatest in white lupin and smallest in wheat whereas total P was lowest in white lupin residues (Table 4). Correspondingly, the amount of N added with the residues was highest in white lupin and lowest in wheat.

Wheat biomass, N and P uptake

The shoot biomass of wheat was greater in the neutral Monarto and alkaline Langhorne creek soil than in the acidic Mount Bold soil (Fig. 1a). In the alkaline Langhorne Creek soil, shoot biomass was greater in previously cropped soil than in previously unplanted soil. This was also the case in the neutral Monarto soil for the pre-crops white lupin and wheat but not for faba bean. In these two soils, addition of residues to previously unplanted soil did not increase wheat growth compared to the unplanted and un-amended soils. The shoot dry weight was similar in all treatments in the acidic Mount Bold soil. The root dry weight ranged between 0.1 and 0.5 g pot^{-1} and was lower in the acidic Mount Bold soil than in the other two soils (data not shown).

Addition of residues to previously unplanted soil did not increase wheat shoot P concentration in any of the soils (Fig. 1b). But faba bean pre-crop (in the alkaline Langhorne Creek and neutral Monarto soil) and white lupin pre-crop (in the neutral Monarto soil) increased wheat shoot P concentrations. In the

Table 4 Shoot and root dry weight of pre-crops (phase 1; average of the three soils, $n=12$) and concentrations of total N and P in residues of faba bean, white lupin and wheat pre-crops ($n=3$)

	Pre-crop		Residue	
	Shoot dw (g $plant^{-1}$)	Root dw	Total N (g kg^{-1})	Total P
Faba bean	1.5	1.5	24.1	1.6
White lupin	1.0	0.4	28.2	1.3
Wheat	0.8	0.3	17.1	1.7
Lsd	0.3	0.2	6.9	0.3

acidic Mount Bold soil, shoot P concentration was highest in the previously unplanted soil without residues and the faba bean pre-crop soil and lowest in wheat pre-crop soil. Shoot P uptake showed a similar trend as shoot biomass in the alkaline Langhorne Creek and the neutral Monarto soil whereas in the acidic Mount Bold soil shoot P uptake was highest in previously unplanted soil without residues or with wheat residues and in faba bean pre-crop soil (Fig. 1c).

In the alkaline Langhorne Creek and neutral Monarto soils, wheat shoot N concentration was generally higher with residue addition alone than in pre-crop soils, whereas the reverse was true for shoot N uptake which was highest in wheat pre-crop soil and lowest in faba bean pre-crop soil (Fig. 1d). However, there were no differences among treatments in shoot N concentration and N uptake in the acidic Mount Bold soil (Fig. 1e).

AMF colonization

The AMF colonization of the wheat roots ranged between 16 and 57 % and did not differ among soils (Fig. 1f). In the neutral Langhorne Creek and the acidic Mount Bold soil, AMF colonization was highest in previously unplanted soil and in all soils it was lowest in white lupin pre-crop soil. In all soils, AMF colonization was negatively correlated with resin P: r=-0.42, -0.75, -0.50 (P<0.05), for the neutral Monarto soil, the alkaline Langhorne creek soil and the acidic Mount Bold soil, respectively.

Soil biochemical properties in the rhizosphere of wheat

The pH in the rhizosphere of wheat showed the same trends as in the original soils, being highest in the

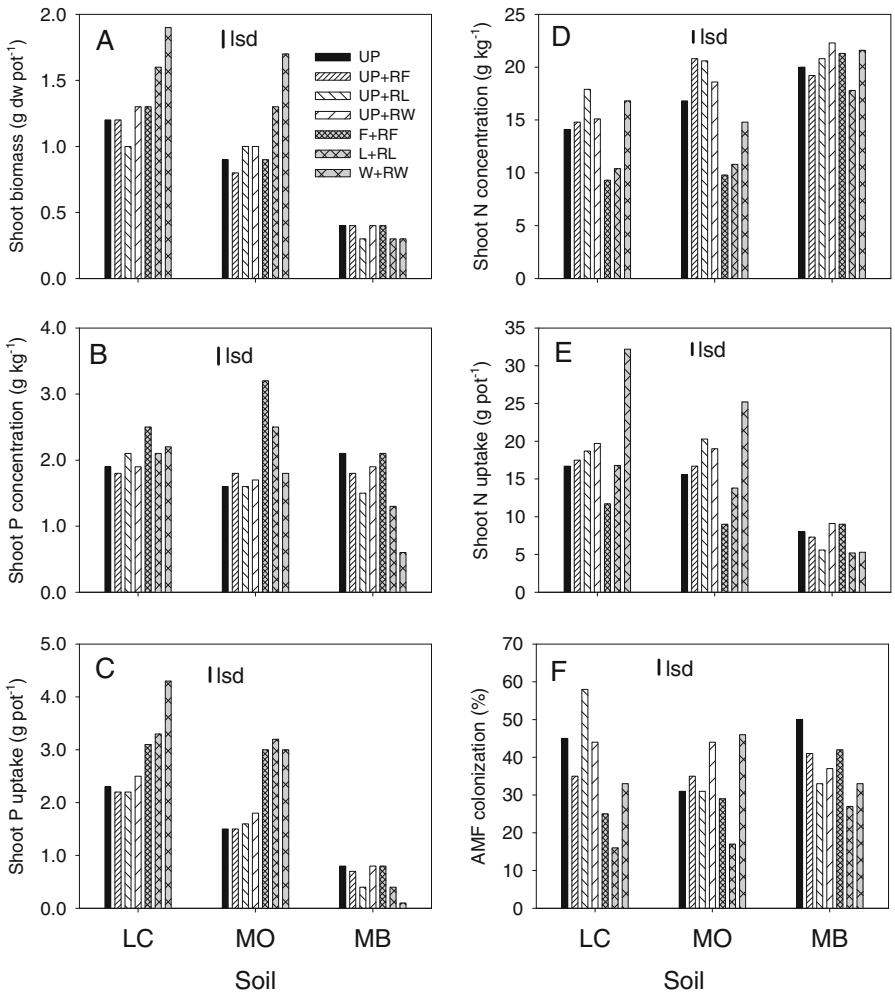


Fig. 1 Shoot dry weight **a**, shoot P concentration **b** and uptake **c**, N concentration **d** and uptake **e** and AMF colonization **f** of wheat in the second phase of the rotation in the alkaline Langhorne Creek (*LC*), the neutral Monarto (*MO*) and the acidic Mount Bold (*MB*) soils. The vertical lines represent the least significant difference (n=4)

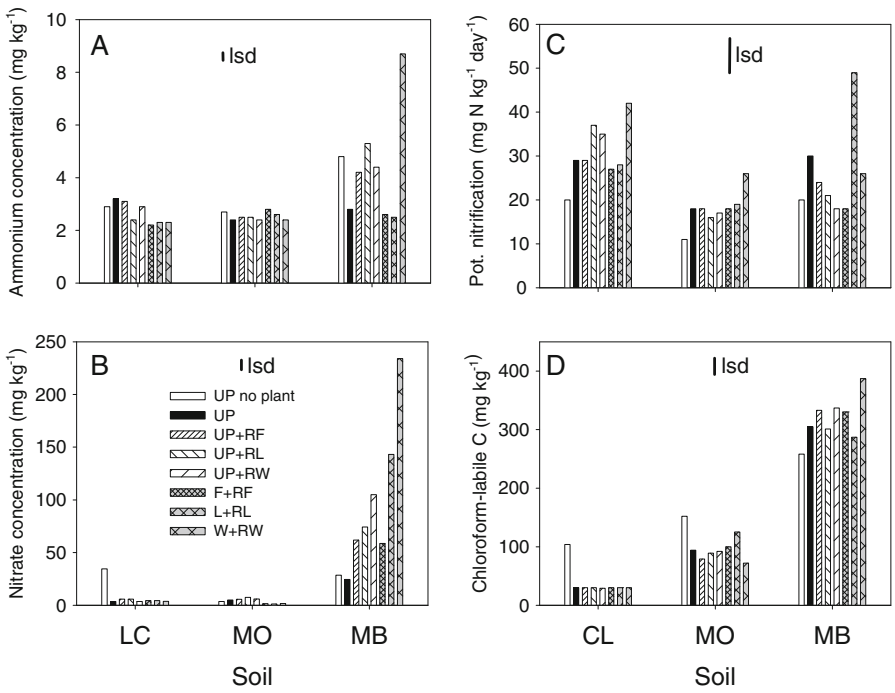


Fig. 2 Rhizosphere soil ammonium **a**, nitrate concentrations **b**, potential nitrification activity **c** and chloroform-labile C **d** in the bulk soil and previously unplanted soil in the alkaline Langhorne Creek (*LH*), the neutral Monarto (*MO*) and the acidic Mount Bold (*MB*) soils. The vertical lines represent the least significant difference (n=4)

alkaline Langhorne Creek soil and lowest in acidic Mount Bold soil (data not shown). In all three soils it was lowest in the rhizosphere of wheat after wheat pre-crop and generally lower in previously cropped soil compared to previously unplanted soil.

The ammonium and particularly the nitrate concentrations were higher in the acidic Mount Bold soil than in the other two soils (Fig. 2a, b). In the neutral Langhorne Creek soil, the ammonium and nitrate concentrations did not differ among treatments. In the neutral Monarto soil, the ammonium concentration was highest in faba bean pre-crop soil whereas the nitrate concentration was highest in the previously unplanted soil with residues. In acidic Mount Bold soil, ammonium and nitrate concentrations were highest in wheat pre-crop soil.

The potential nitrification activity (PNA) was highest in wheat pre-crop soil and lowest in previously unplanted soil in Monarto and Langhorne Creek soils (Fig. 2c), whereas in Mount Bold it was highest in white lupin pre-crop soil. The PNA was negatively correlated with soil nitrate concentration only in the neutral Monarto soil (r=-0.55, P<0.01).

The chloroform-labile C concentration was highest in the acidic Mount Bold soil (Fig. 2d). In the alkaline Langhorne Creek and the neutral Monarto soil, it was highest in the previously unplanted soil without residues whereas in the acidic Mt Bold soil, it was lowest in the previously unplanted soil and the white lupin pre-crop soil and highest in the wheat pre-crop soil. In general, residue addition had no significant effect on the chloroform-labile C concentration.

Microbial community composition

The community composition of ammonium-oxidizing archaea (AOA) and nifH differed among the three soils (Fig. 3, Table 5), while the community composition of bacteria and fungi only differed between the acidic Mount Bold soil on the one side and the neutral Monarto and the alkaline Langhorne Creek soils on the other. The community composition of the ammonium-oxidizing bacteria (AOB) in the neutral Monarto soil was different from that in the alkaline Langhorne Creek soil (AOB could not be amplified in the acidic Mount Bold soil).

Based on the PERMANOVA results, the community composition of the investigated microbial groups in all three soils differed between the soil without wheat and the rhizosphere soil (Fig. 3, Table 5). Residue addition or pre-crop had little effect on community composition with a few exceptions. The ALP gene composition differed between wheat grown in faba bean pre-crop soil and wheat grown in wheat

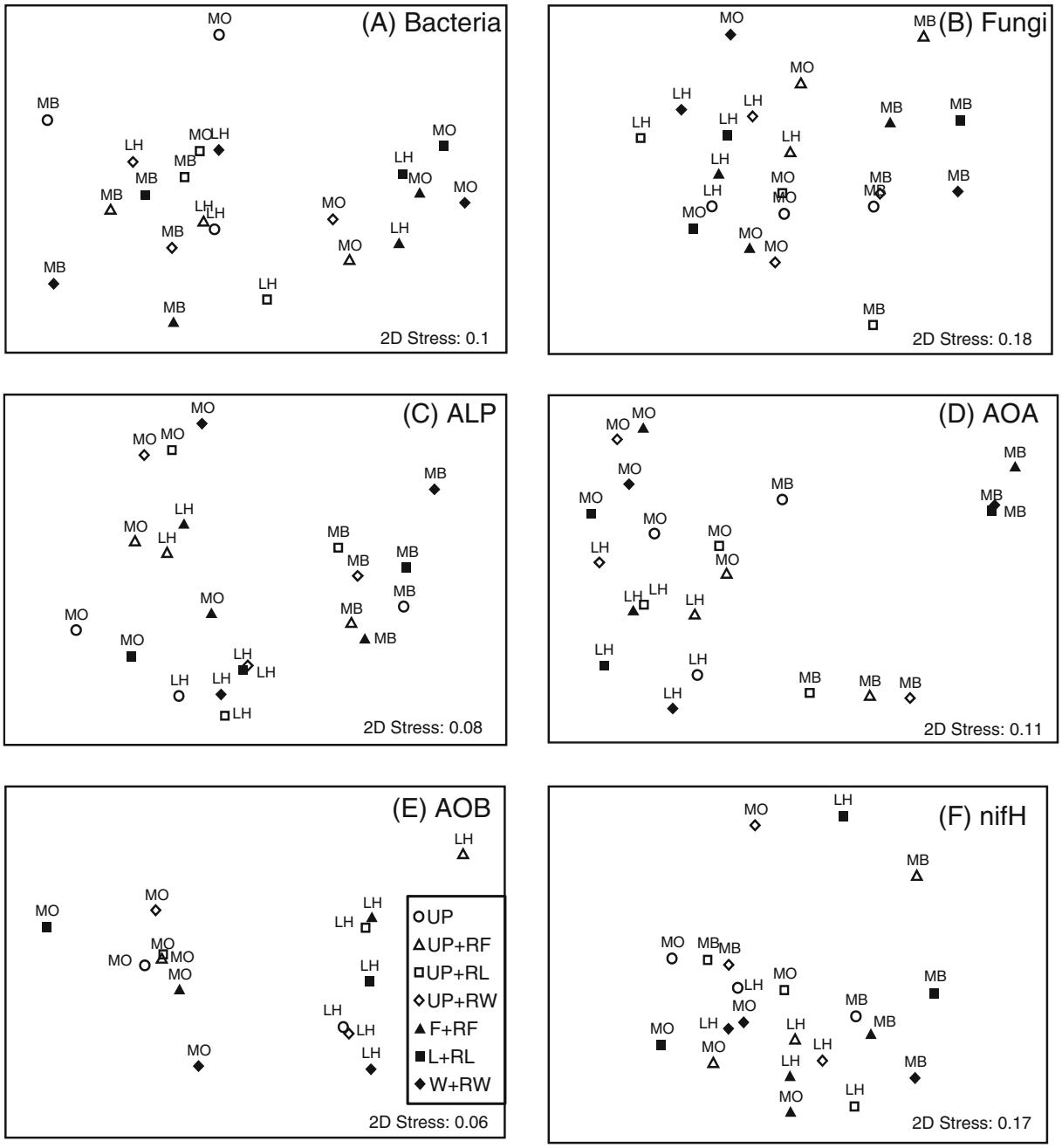


Fig. 3 MDS plots of the community composition of bacteria **a**, fungi **b**, ALP gene **c**, ammonium-oxidizing archaea **d**, ammonium-oxidizing bacteria **e** and N_2-fixers (NifH) **f** in the rhizosphere of wheat in phase 2 of the rotation in the alkaline Langhorne Creek (*LH*), the neutral Monarto (*MO*) and the acidic Mount Bold (*MB*) soils. Symbols represent averages of four replicates

pre-crop soil. In the alkaline Langhorne Creek and the neutral Monarto soil, the nifH community was different in faba bean and white lupin pre-crop soil compared to wheat pre-crop soil and previously unplanted soil with or without residues. In the acidic Mount Bold soil on the other hand, the nifH community composition in the pre-crop soil was different from that in previously unplanted soil with residues. Additionally, the nifH community in previously unplanted soil without residues or with wheat residues differed from that

with legume residues. In the alkaline Langhorne Creek soil, the AOB community composition was affected by pre-crops with legumes differing from wheat and by residue addition; wheat residue addition resulting in a different community composition than the legume residues. In the neutral Monarto soil, the AOA community composition in legume pre-crop soil was different from that in previously unplanted soil with or without residues.

Soil P pools in the rhizosphere of wheat

In the alkaline Langhorne creek soil, the concentrations of $NaHCO_3$ Pi and HCl Pi were higher than in the rhizosphere of wheat grown in the neutral Monarto and the acidic Mount Bold soil, whereas the concentrations of $NaHCO_3$ Po, NaOH I Pi, NaOH I Po, residual P and total P were higher in the acidic Mount Bold soil than the other two soils (Fig. 4, only showing P pools with significant soil x treatment interactions). The concentrations of the labile resin P and $NaHCO_3$ P, as well as of the less labile NaOH I P were generally higher in wheat grown in the pre-crop soils compared to wheat grown in the previously unplanted soil.

Fig. 4 Concentrations of resin P **a**, microbial P **b**, $NaHCO_3$ Pi **c** $NaHCO_3$ Po **d**, NaOH I Pi **e**, NaOH I Po **f**, HCl Pi **g** and residual P **h** in the rhizosphere of wheat and the unplanted soil in phase 2 of the rotation in the alkaline Langhorne Creek (*LH*), the neutral Monarto (*MO*) and the acidic Mount Bold (*MB*) soils. The vertical lines represent the least significant difference (n=4)

In the alkaline Langhorne Creek and the neutral Monarto soil, the resin P concentration was highest in the rhizosphere of wheat grown in faba bean pre-crop soil and lowest in wheat grown previously unplanted soil without residues (Fig. 4a). Residue addition to the previously unplanted soil decreased resin P. In the acidic Mount Bold soil, the resin P concentration was lowest in wheat grown in the previously unplanted soil and highest in wheat grown in wheat pre-crop soil.

In the alkaline Langhorne Creek and the neutral Monarto soil, microbial P was lowest in the rhizosphere of wheat grown in previously unplanted soil without residues and the soil without wheat plants and highest in wheat grown in white lupin pre-crop soil (Fig. 4b). Residue addition to the previously unplanted soil and pre-crop soils increased microbial P. In the acidic Mount Bold soil, microbial P was generally higher in wheat grown in the previously unplanted soil with residues

Table 5 Significant differences in community composition of different microbial groups ($P \leq 0.05$, indicated by ≠) in the three soils based on PERMANOVA

Group	Among soils	Alkaline Langhorne Creek	Neutral Monarto	Acidic Mount Bold
Bacteria	MB≠LC, MO	UP≠R	UP≠R	UP≠R
Fungi	MB≠LC, MO	UP≠R	UP≠R	UP≠R
ALP	MB≠LC≠MO	UP≠R F+RF≠W+RW	UP≠R F+RF≠W+RW	UP≠R
AOA	MB≠LC≠MO	UP≠R	UP≠R F+RF, L+RL≠UP±residues	UP≠R
AOB	LC≠MO	UP≠R UP+RW≠UP+RF, UP+RL W+RW≠F+RF, L+RL	UP≠R	UP≠R
nifH	MB≠LC≠MO	UP≠R F+RF, L+RL≠ W+RW, U±residues	UP≠R F+RF, L+RL ≠ W+RW, UP±residues	UP≠R Pre-crop≠U residues UP, UP+RW≠UP+RF, UP+RL

ALP alkaline phosphatase genes

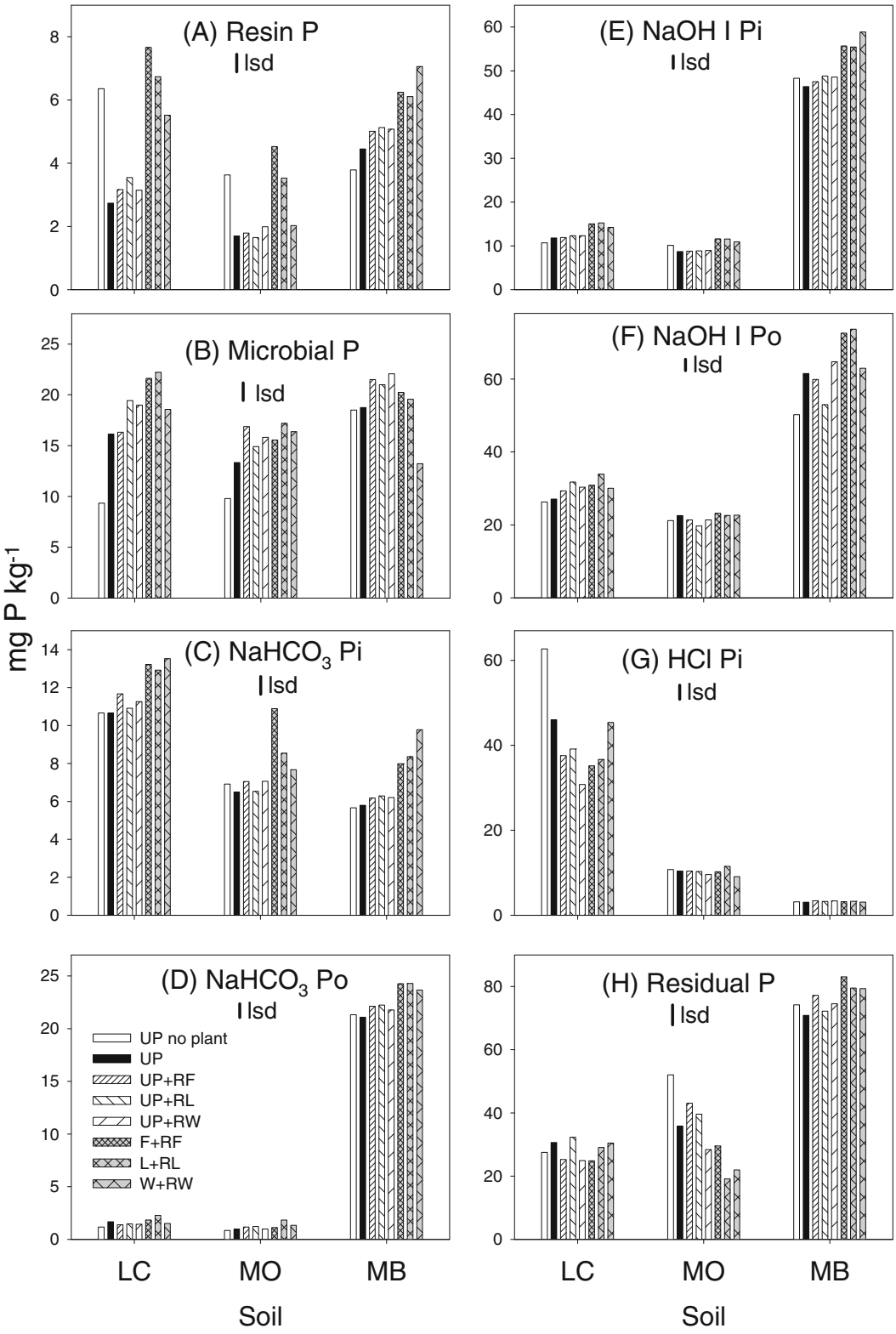
AOA ammonia-oxidizing archaea

AOB ammonia-oxidizing bacteria

nifH nitrogen-fixing genes

LC, *MO*, *MB* soil from Langhorne Creek, Monarto, Mount Bold

UP, *R* unplanted soil, rhizosphere soil


(A) Resin P
lsd
(E) NaOH I Pi
lsd
(B) Microbial P
lsd
(F) NaOH I Po
lsd
(C) NaHCO3 Pi
lsd
(G) HCl Pi
lsd
(D) NaHCO3 Po
lsd
(H) Residual P
lsd
mg P kg-1
UP no plant
UP
UP+RF
UP+RL
UP+RW
F+RF
L+RL
W+RW
LC
MO
MB
Soil

than that in wheat grown in pre-crop soils with residues and wheat grown in previously unplanted soil without residues, except for faba bean pre-crop soil.

The concentrations of $NaHCO_3$ Pi and NaOH I Pi in the rhizosphere of wheat were not affected by residue addition to previously unplanted soil in the three soils (Fig. 4c, e). Among the pre-crops, the concentration of $NaHCO_3$ Pi was highest in wheat grown in faba bean pre-crop soil in neutral Monarto soil, but highest in wheat grown in wheat pre-crop soil in the acidic Mount Bold soil (Fig. 4c). In the alkaline Langhorne Creek soil, the $NaHCO_3$-Po concentration was lower in wheat grown in the wheat pre-crop soil than in the other pre-crop soils (Fig. 4d). This was also true for the NaOH I Po concentration in the acidic Mount Bold soil (Fig. 4f).

The concentration of HCl Pi in the alkaline Langhorne Creek soil was highest in previously unplanted soil without wheat plants and lowest in wheat grown in previously unplanted soil with wheat residues. In the neutral Monarto and the acidic Mount Bold soil, the concentration of HCl Pi was similar in all treatments (Fig. 4g).

The concentration of residual P in the alkaline Langhorne Creek soil was lowest in wheat grown in the faba bean treatments (faba bean residues in previously unplanted soil or faba bean pre-crop) (Fig. 4h). In the neutral Monarto soil, residual P was lower in wheat grown in pre-crop soils compared to wheat grown in previously unplanted soil and was lowest in white lupin pre-crop soil. In the acidic Mount Bold soil on the other hand, wheat grown in pre-crop soils had a higher concentration of residual P than wheat grown in the previously unplanted soil.

The concentrations of the NaOH II and concentrated HCl P pools differed only among soils (data not shown). Whereas the concentration of NaOH II Pi was higher in the acidic Mount Bold soil than in the other two soils, the concentration of NaOH Po was highest in the alkaline Langhorne Creek soil. The concentration of concentrated HCl Pi was highest in the neutral Monarto and lowest in the alkaline Langhorne Creek soil whereas the concentration of concentrated HCl Po was highest in the alkaline Langhorne Creek soil and lowest in the acidic Mount Bold soil.

Discussion

This study showed that wheat growth and P uptake as well as rhizosphere P pools and microbial community composition are affected mainly by soil type but also by pre-crops and their residues with residue addition to previously unplanted soil generally having little effect.

Wheat growth and P uptake

Wheat shoot and root biomass were highest in the alkaline Langhorne Creek soil and lowest in the acidic Mount Bold soil. This can be explained by the higher potentially available P (resin P and $NaHCO_3$ Pi) in the alkaline Langhorne Creek soil than the other two soils. There were no differences in root and shoot biomass among treatments in the acidic Mount Bold soil, but in both the alkaline Langhorne Creek and the neutral Monarto soil, shoot biomass was highest in wheat grown in wheat and white lupin pre-crop soils which may be due to the higher concentrations of potentially available P pools (resin P, $NaHCO_3$) in these treatments. Wheat shoot P concentration was highest when grown in faba bean pre-crop soil in all three soils. This is in agreement with previous studies in which wheat after faba bean had a higher P concentration compared to wheat after other legumes and wheat pre-crops (Nuruzzaman et al. 2005). However, the high shoot P concentration is most likely a consequence of the poor growth of wheat in faba bean pre-crop soil indicating that another factor is limiting wheat growth, for example compounds released during faba bean residue decomposition that inhibit wheat growth.

Differences in soil P pools among soils

The soils differed in concentrations of the various P pools. The alkaline Langhorne Creek soil had the highest concentrations of HCl P whereas the concentrations of NaOH I Pi+Po, NaOH II Pi, residual P and total P were highest in the acidic Mount Bold soil. This can be explained by the differences in pH among the soils, as P bound to Fe and Al oxides (NaOH P) is dominant in acidic soils and Ca bound phosphates (HCl P) are dominant in alkaline soils (Frossard et al. 1995; Hinsinger 2001; Lindsay 1979). However, there were also some differences between soils which can not be explained by pH, such as the higher concentrations of NaOH II Po in the neutral Langhorne Creek soil and of concentrated HCl Pi in the acidic Mount Bold soil. This might be due to differential soil parent material which affects soil Al, Fe, Ca concentrations (Renneson et al. 2010) or soil texture which

may affect transfer of P between pools (Chardon and Schoumans 2007; Renneson et al. 2010).

In the alkaline Langhorne Creek and neutral Monarto soil, the presence of wheat plants and residue addition increased soil microbial P which can be explained by the easily available C released into the rhizosphere (Marschner et al. 2006) and from residues (Saffigna et al. 1989). On the other hand, there was no rhizosphere or residue effect on microbial P in the acidic Mount Bold soil. The high soil organic matter content in this soil may have provided sufficient C to over-ride a rhizosphere effect. This interpretation is supported by the high concentration of chloroform-labile C in the Mount Bold soil.

The small amount of residues added was (1 gkg^{-1}) can explain the small effect of the residues alone on soil P pools. Despite the low addition rate, the decrease in resin P and the corresponding increase in microbial P shows that P was immobilized which can be explained by their total P concentration which varied from 1.3 to 1.7 gkg^{-1}. This is below 2-3 gkg^{-1} which was the threshold for P immobilization in a previous study (Yadvinder-Singh and Khind 1992).

In the soil with residues, the presence of plants in phase 1 of the rotation increased the concentrations of labile P pools and the NaOH extractable P pools in the rhizosphere of the following wheat compared to the previously unplanted soil with the increase occurring in both inorganic and organic P fractions which could be due to mobilization of P during the pre-crop phase. In the alkaline Langhorne Creek and the neutral Monarto soil, labile P accumulated in the rhizosphere although the plants grew better and took up more P in pre-crop soil compared to previously unplanted soil. This indicates that more P was mobilized than was required by the wheat.

The finding that pre-crops not only increased the inorganic but also the organic P fractions of the $NaHCO_3$ and NaOH pools suggests conversion of inorganic into organic P by soil microbes stimulated by root exudates and dead roots (Rangel-Castro et al. 2005). The origin of the increased P concentrations in the $NaHCO_3$ and NaOH pools appears to differ among soils. In the alkaline Langhorne Creek soil, the lower concentration of HCl Pi in pre-crop soil suggests that P from this pool was converted into the $NaHCO_3$ and NaOH pools. In the neutral Monarto soil, the source of the increased P concentrations in the $NaHCO_3$ and NaOH pools appears to be residual P as this P pool was lower in pre-crop soil compared to previously unplanted soil. However in the acidic Mount Bold soil, neither HCl P nor residual P were lower in pre-crop soil. Therefore it is not clear where the increased P concentration in the $NaHCO_3$ and NaOH pools originated in this soil.

In a previous study with the same soils in which faba bean, white lupin and wheat were grown in monoculture or in mixed culture of wheat with legumes (Wang et al. 2011, in press), plant growth and rhizosphere microbial community composition and soil P pools were also predominately affected by soil type whereas the cropping system (monoculture versus mixed culture) had little effect. In that study, wheat and legumes depleted less labile inorganic P whereas less labile organic P accumulated in the rhizosphere of the legumes. In the present study, both labile and non-labile P pools accumulated in the rhizosphere of wheat in phase 2 and there were little differences in P pools among the soils from different pre-crops. Thus, the differential depletion or accumulation of inorganic and organic P pools between legumes and wheat does not have a strong effect on the concentrations of P pools in the rhizosphere of the following wheat.

Mycorrhizal colonization

Mycorrhizal hyphae can increase the soil volume accessible to plants and thereby increase plant P uptake (Smith et al. 2001). In the present study, AMF colonization of wheat ranged from 16 % to 57 % and was similar in all soils. In accordance with previous studies, AMF colonization of wheat was negatively correlated with soil available P (Jensen and Jakobsen 1980). However, among the pre-crops, white lupin had the strongest negative effect on AMF colonization although resin P concentrations were not higher than in the other pre-crop soils. This may be due to the fact that white lupin is considered to be a non-mycorrhizal plant (Keerthisinghe et al. 1998). Negative effects of non-mycorrhizal crops on the colonization of the following crop have been reported before (Haymann et al. 1975; Powell 1982). Compared to soil without residues, decreased AMF colonization of wheat was found with addition of faba bean residues in the alkaline Langhorne Creek and the acidic Mount Bold soil and of white lupin residues in the acidic Mount Bold soil. In a previous study, Hasbullah and McNeill

(2011) also found negative effects of legume residues on AMF colonization of wheat which was not related to available P concentrations.

Conclusion

This study showed that the main factor affecting wheat growth, soil P pools and microbial community composition was the soil pH. Within a given soil, legume pre-crops also influenced wheat growth and soil P pools, but their effect varied with soil type. In general, pre-crops increased the concentrations of labile and non-labile P pools in the rhizosphere of the following wheat and stimulated wheat growth and P uptake. The elevated concentrations of labile P in the rhizosphere after 6 weeks suggest that pre-crops may also provide P for wheat in the later stages of growth, but this would have to be tested by growing wheat in phase 2 to maturity. Addition of residues alone had little effect on soil P pools or wheat growth which may be related to the low addition rates used here. However, the negative effect of some residues even at these low rates suggest that adding more residues could reduce wheat growth despite supplying more P.

This results further suggests that studying soil P pools is unlikely to provide clear explanations of the effect of the pre-crops on P uptake by wheat across soil types. In terms of management to enhance P availability to cereals, the optimal rotation is soil pH-dependent with white lupin and wheat being more effective than faba bean in the alkaline and neutral soil, but not in the acidic soil.

Acknowledgments We thank Collin Rivers for his help in collecting soil from Monarto and Mount Bold and Sean Mason for collecting soil from Langhorne Creek. We are grateful to the financial support from the Australian Research Council, and the China Scholarship Council.

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