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Soil phosphorus pools in the detritusphere of plant residues with different C/P ratio—influence of drying and rewetting

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Abstract

Little is known about the effect of drying and rewetting (DRW) on phosphorus (P) pools in the detritusphere, the soil adjacent to plant residues. Two plant residues differing in their potential to release P during decomposition were used: mature barley straw, C/P 255 or young faba bean, C/P 38. Residues were placed between two PVC caps filled with soil at 50% water-holding capacity with open ends covered by fine mesh onto which the residues were placed. The open ends of the two PVC caps were pressed together with residues in between. For the unamended controls, no residues were placed between the meshes. After 2 weeks incubation, the soil was separated from the residues and then either dried and kept dry for 2 weeks followed by rapid rewetting to 50% water-holding capacity (WHC) rewetting (RW) or maintained at 50% of WHC constantly moist (CM). Bioavailable P pools (readily available P pools: $CaCl_2$- and anion exchange-P; P bound to soil particles: citrate- and HCl-P; acid phosphomonoesterase- and microbial-P) were measured in dry soil and 1, 7, and 14 days after rewetting. Rewetting of dry soils induced a respiration flush on the first day after which respiration rates declined to those in CM. Compared to the unamended soil, the flush was about 75% higher with barley and more than twofold higher with faba bean. P pools were 3–20-fold higher with faba bean than with barley or in the control. At the end of the dry period, most P pools were higher in dry soil compared to CM. Rewetting had little effect on P pools 1, 7, and 14 days after rewetting compared to CM. To investigate if rewetting induced a short pulse of available P, a second experiment was carried out. As in the first experiment, faba bean detritusphere soil and control were generated and then dried or kept at 50% WHC for 2 weeks. Before rewetting, anion exchange membranes (AEM) were placed in the soil which were removed one, 2 or 4 days after rewetting. The P concentration on the AEM was more than threefold higher with faba bean than the control. One day after rewetting, the P concentration on the AEM with faba bean was about threefold higher in RW than in CM, but did not differ between RW and CM in the control. Four days after rewetting, nearly all P pools with faba bean were 10–30% lower in RW than in CM, except citrate-P which was about 5% higher in RW. We conclude that rewetting induces a short pulse of available P if the P pool concentration is high as in the detritusphere of faba bean. If P is removed from the soil (by binding to AEM or uptake by plants), rewetting can induce depletion of P pools compared to CM.

Keywords Barley residue · Drought · Faba bean residue · Phosphorus pools · Soil-residue interface

Introduction

Soil moisture is an important regulator of microbial activity and nutrient availability. In dry soil, the water film around aggregates is thin and may be disrupted, limiting nutrient diffusion and thereby reducing microbial activity (Ilstedt et al. 2000). Through its influence on microbial activity, soil moisture also influences the decomposition of organic materials. In Poll et al. (2008), rye residue decomposition was faster in wet compared to dry soil. Further, the rate of soluble substrate diffusion from the decomposing rye residue into adjacent soil was greater in moist soil. Sardans and Peñuelas (2004) found that drought increased total soil soluble P due to increased soluble organic P. In Mediterranean climates during summer, long dry periods are interrupted by occasional rainfall events. Rewetting of dry soil results in a flush of mineralisation (Borken and Matzner 2009; Inglima et al. 2009; Barnard et al. 2013), with initial short-term flushes of C, N and P (Nguyen and Marschner 2005). Compared to moist soil, rewetting of dry soil has been shown to result in a rapid increase of available P (Butterly et al. 2009; Bünemann et al. 2013) and microbial-P (Nguyen and Marschner 2005). Turner

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et al. (2003) reported that lysed bacterial cells are the source of a large proportion of the water-extractable organic P after rewetting of dry soil.

During decomposition of organic materials there may be release of P, depending on the C/P ratio of the material. The C/P ratio of organic material added to soil, such as crop residues, has been shown to affect soil P availability and P pools (Dalal 1979). Crop residues with C/P > 200 induce net P immobilisation and depletion of soil P pools, whereas residues with lower C/P ratio increase P availability and P pools in soil (Umrit and Friesen 1994; Alamgir et al. 2012). The increase in P availability in soil with decomposing residue can be explained by (i) P release from the residues, (ii) organic acid anions produced during residue decomposition which exchange of sorbed P with (Bolan et al. 1994; Hue et al. 1994), enhance dissolution of phosphate compounds (Bolan et al. 1994) and form complexes with metals. In Alamgir and Marschner (2013), mixing residue (at 20 g kg^{-1} soil) with low C/P ratio (63; faba bean) or medium C/P ratio (232; chickpea) into soil strongly increased labile P pools, resin-P, microbial-P and $NaHCO_3$-extractable inorganic P compared to unamended soil. In contrast, addition of residue with a high C/P ratio (640; white lupin) had little effect on the concentrations of these labile P pools.

The detritusphere (i.e. the soil-litter interface) is defined as a thin layer of soil, usually < 5 mm, directly adjacent to litter and influenced by litter decomposition (Liu et al. 2011). The detritusphere, like the rhizosphere, is characterised by high concentrations of easily available compounds, especially in the early stage of residue decomposition when water-soluble compounds are released (Poll et al. 2010). For example, Gaillard et al. (1999) found increased enzyme activities and litter-derived C within a distance of 3–4 mm from the litter. Compared to bulk soil, detritusphere soil has been shown to have increased C and N turnover (Kandeler et al. 1999) and abundance of bacteria and fungi (Marschner et al. 2012). Increased C mineralisation can increase P release by increasing the mineralisation of organic P (Wang et al. 2016).

The concentration of extractable P in the soil directly adjacent the decomposing residue may be higher than that in bulk soil. For example, in de Neergaard and Magid (2015), extractable P was higher in detritusphere soil up to 3 mm from the residue layer than bulk soil. The higher extractable P corresponded to about 20% of the P lost from the plant residue. Ha et al. (2007) studied P release during decomposition of legume residues with different C/P ratio (young legume with low C/P ratio or mature legume with high C/P ratio) in soil. They found that from 5 days after residue placement, microbial P was greater in the immediate vicinity of the residues (< 5 mm) compared to the bulk soil. Resin-extractable P was significantly higher in the vicinity of the young legume residue compared to the mature legume and the bulk soil.

The effect of residue C/P ratio on P pools is well-known, but previous studies have been carried out in constantly moist soil. Little is known about the effect of soil moisture on P pools in the detritusphere of crop residues with differing C/P ratios. The aim of this study was to determine P pools in detritusphere soil of two crop residues with different C/P ratios maintained constantly moist or dried and rewet. Shoot residues of young faba bean with a low C/P ratio (C/P 38), and mature barley straw with a high C/P ratio (C/P 255) were used in this study to generate the detritusphere soils for 2 weeks. Controls were soils incubated in the same manner without residues. Control and detritusphere soils were then exposed to a drying and rewetting cycle or maintained moist. We hypothesised that (1) rapid rewetting will induce a transient increase in available P pools compared to constantly moist soils, but have little effect on more stable soil P pools, and (2) the influence of rewetting on available P will increase in the following order control < detritusphere soil of high C/P < low C/P residue. To address these hypotheses, detritusphere was generated. After residue removal, detritusphere soils were used in three experiments. In the first experiment, the effect of drying and rewetting on P pools in detritusphere soil of high and low C/P residues was studied. The expected flush of available P was not observed 1 day after rewetting. A second experiment was carried out to assess if there was a short-term increase of available P using anion exchange membranes to capture released P. The anion exchange membranes adsorbed P released upon rewetting, but P concentration on the membranes decreased over time. Therefore, a third experiment was carried out to assess P loss from the anion exchange membranes.

Materials and methods

Soil and plant residues

A loamy sand was collected from 0 to 10 cm on Waite Campus, The University of Adelaide, South Australia (Longitude 138° 38′ E, Latitude 35° 6′ S) which had been under permanent pasture over 80 years. This area has a Mediterranean climate, characterised by cool, wet winters and hot, dry summers occasionally interrupted by rainfall events. The soil is a Red-brown Earth according to Australian soil classification (Isbell 2002) and is classified as Rhodoxeralf in US Soil Taxonomy (Chittleborough and Oades 1979). At the sampling site, soil was collected at six randomly chosen locations and pooled to one composite sample. The soil was dried at 40 °C and passed through a 2-mm sieve. The properties of the soil are as follows: clay 250 g kg^{-1}; sand 370 g kg^{-1}; silt 380 g kg^{-1}; total P 302 mg kg^{-1}; pH (1:5 soil: water) 5.6; EC (1:5) 0.1 dS m^{-1}; total organic C 17 g kg^{-1}; total N 1.5 g kg^{-1}; bulk density

1.3 g cm^{-3}; maximum water-holding capacity (WHC) 349 g kg^{-1}.

Two types of crop residues were used: young faba bean shoots (*Vicia faba* L.) as a low C/P residue (38), and mature barley straw (*Hordeum vulgare* L.) as high C/P residue (255) which are commonly grown in Southern Australia. The residues were dried at 40 °C in a fan-forced oven, ground and sieved to 0.25−2.00-mm particle size. Total N and P were about eight- and fourfold higher, respectively, in young faba bean shoots than mature barley straw (Table 1). Water-soluble P was about 60-fold higher in faba bean residues than straw.

Experimental design

Microcosm setup

The microcosms used were as described in Ha et al. (2007). Caps of PVC tubes (height 20 mm, diameter 70 mm) were filled with 90 g of dry soil which was packed to a bulk density of 1.3 g cm^{-1}. The soil was incubated for 7 days at 20−25°C in the dark at 50% WHC to activate the soil microbes and to stabilise respiration after rewetting of air-dry soil. Then, fine nylon mesh (mesh size 0.1 mm × 0.8 mm) was cut into circles with a diameter of 85 mm and placed over the soil to cover the open side of each cap. Ground and sieved crop residues (3.6 g per microcosm, equivalent to 20 g kg^{-1}) were placed in a thin layer between two layers of mesh covering the entire area. Then, the two open ends were pressed together with the two caps held together with rubber bands thereby avoiding loss of residue during the experiment. The control was without residue between the meshes. The microcosms were incubated at 20−25 °C in the dark for 2 weeks during which soil moisture was maintained at 50% WHC by weight. The closed ends of the caps had four holes through which water could be added to maintain the soil water content and which allowed gas exchange. Two weeks was chosen based on a preliminary study, which showed that P pools in the detritusphere soil changed little after 2 weeks incubation (data not shown). After 2 weeks, the two PVC caps were carefully separated from each other and the two layers of mesh with the residues in between removed without disturbing the soil surface. Soil at 0–2-mm distance from the surface was collected as the detritusphere soil. Fifteen grams of soil was collected from each PVC cap of a given microcosm which were pooled to get 30 g per replicate for the following periods.

Table 1 Total organic C, N, P, C/N ratio and C/P ratio of high C/P (mature barley straw) and low C/P (young faba bean shoot) residues ($n = 4$). Different letters indicate significant differences between residues ($P \geq 0.05$)

Properties	High C/P	Low C/P
Total organic C (g kg^{-1})	408b	347a
Total N (g kg^{-1})	4.3a	38.5b
Total P (g kg^{-1})	1.7a	9.2b
Water-extractable P (g kg^{-1})	0.1a	6.5b
C/P ratio	255b	38a
C/N ratio	95b	9a

Effect of DRW on microbial activity and P pools in detritusphere of high and low C/P residues (experiment 1)

The first experiment aimed to assess how the P pools were influenced by drying and rewetting (DRW). It was conducted with detritusphere soils of faba bean or barley residue, and control soil without residue.

Detritusphere soil (30 g, generated as described above and after removal of residues) was filled into PVC containers (1.85-cm radius, 5-cm height) with a nylon mesh base (7.5 μm, Australian Filter Specialist) and packed to a bulk density of 1.3 g cm^{-1}. The cores were placed individually into 1-L jars with gas-tight lids equipped with septa to allow quantification of the headspace CO_2 concentration as described below. The jars were incubated in the dark at 20−25 °C. To dry the soil, two pouches of self-indicating silica gel (BDH Chemicals, 8 g per pouch) were placed in each jar, and exchanged daily. The soil was dried to approx. 5% WHC (after 4 days) after which the soil was maintained dry for another 10 days (total dry period of 14 days). Then, dry soils were rapidly rewetted to 50% WHC with reverse osmosis (RO) water and incubated at this water content for 2 weeks. Constantly moist control soil was maintained at 50% WHC throughout. Cores were destructively sampled for analyses 1 day before rewetting, and 1, 7 and 14 days after rewetting.

Effect of DRW and P removal by AEM on detritusphere P pools (experiment 2)

In the first experiment, the effect of DRW on P pools was small and no flush of available P was observed. Based on previous studies (e.g. Butterly et al. 2009; Bünemann et al. 2013), rewetting probably induced release of P, but the released P was rapidly sorbed so that the flush was not apparent 1 day after rewetting. On the other hand, plant uptake can strongly deplete available P as well as other P pools (Hoang and Marschner 2017). To determine the effect of DRW on P release, as related to plant uptake, a second experiment was carried out, using anion exchange membranes to mimic the removal of P from soil operated by plants. In this experiment, only detritusphere soil of faba bean residue was compared with the control soil, because in the first experiment, P pools in the detritusphere of faba bean were higher than that in the control soil, but differed little between barley detritusphere

and control. We assumed that P release and thus P captured by the anion exchange membranes would be measurable, at least in faba bean soil. Detritusphere soil of faba bean residue or the control soil was filled into PVC containers, as described above and then dried and kept dry for 14 days. Constantly moist soil was maintained at 50% WHC throughout. Anion exchange membranes (three strips, approximately 6 × 2 cm each) were inserted into each of the soil containers, and the dry soils were rapidly rewetted to 50% WHC with RO water. The resin membranes were removed from the containers 1, 2 and 4 days after rewetting. P concentration on the strips was measured at each time, and P pools in the soil were determined after 4 days.

P loss from pre-loaded AEM strips (experiment 3)

In the second experiment, especially in the faba bean detritusphere soil, the P concentration on the anion exchange membranes was lower on day 4 than that on day 1. In order to confirm this loss of P from the anion exchange membranes, a third experiment was carried out. In this experiment, anion exchange membranes were loaded with P by shaking them in 0.3 mg $P{\cdot}L^{-1}$ for 17 h. Constantly moist control soil was placed in PVC cores as described above. The P-loaded membranes were inserted into the soil (three strips per 30 g of soil per container) and then removed 1, 2 and 4 days after rewetting. P concentration on the membranes was determined.

Analytical methods

Soil maximum WHC was measured in a sintered glass funnel connected to a 1-m water column (matric potential − 10 kPa) (Wilke 2005). Soil texture was determined by the hydrometer method (Ge and Or 2002). Soil pH was determined in a 1:5 (*w*/*v*) soil to reverse osmosis (RO) water ratio after 1 h end-over-end shaking (Rayment and Higginson 1992). Total organic C of soil and plant residues was determined by wet oxidation with $K_2Cr_2O_7$ and H_2SO_4, followed by back-titration with $(NH_4)_2Fe(SO_4)_2{\cdot}6H_2O$ (Walkley and Black 1934). Total N in soil and plant residues was extracted and determined by the Kjeldahl method (McKenzie and Wallace 1954). To determine total P, soil and plant residues were digested with a mixture of HNO_3 and $HClO_4$. Total P in the extract was measured by the phosphovanadomolybdate method (Hanson 1950). Water-soluble P in the residues was extracted with hot water as described by Konieczynski and Wesolowski (2007) with minor modification. To 1 g residue, 30 mL of hot (85 °C) RO water were added, then shaken for 2 h and filtered. The filtrate P concentration was measured colorimetrically (630 nm) using the malachite-green method as described in Ohno and Zibilske (1991).

Soil respiration was measured by quantifying the CO_2 concentration in the headspace of the jars using a Servomex 1450 infra-red analyser (Servomex Group, Crowborough, UK) as described in Setia et al. (2011). Jars were vented with a fan to refresh the headspace after each measurement (t1) and then resealed following another CO_2 measurement (t0). The CO_2 produced during this given interval is the difference in CO_2 concentration between t1 and t0. Linear regression based on injection of known amounts of CO_2 in similar jars was used to define the relationship between CO_2 concentration and detector reading.

Soil P pools were measured as described in DeLuca et al. (2015). Each pool was measured in parallel by shaking 0.5 g of soil with each extractant (10 ml of 10 mM $CaCl_2$, 10 mM citric acid, 0.2 enzyme units acid phosphomonoesterase, or 1 M HCl) in separate 50-mL tubes for 3 h on an end-over-end shaker. An aliquot of the supernatant was used for measuring P colorimetrically (630 nm) using the malachite-green method as described in Ohno and Zibilske (1991).

Two additional P pools were included. Resin-P and microbial biomass P (MBP) were determined with the anion exchange resin method (Kouno et al. 1995), hexanol was used as fumigant. The P concentration was determined colorimetrically at 712 nm (Murphy and Riley 1962). MBP is the difference in P concentration between fumigated and unfumigated soil (Kouno et al. 1995). No conversion factor was used for P because recovery of a P spike in this soil was 98% (Butterly et al. 2010). Available N (exchangeable ammonium and nitrate) concentration was measured after 1 h end-over-end shaker with 2 M KCl in a 1:5 soil extractant ratio. Ammonium-N was determined after Willis et al. (1996), and nitrate-N after Miranda et al. (2001). Microbial biomass N (MBN) was determined by chloroform fumigation extraction with 0.5 M K_2SO_4 at 1:4 soil to extractant ratio (Moore et al. 2000). Ammonium in the extract was determined as described above. Microbial biomass N was calculated as the difference in NH_4^+ concentration between fumigated and non-fumigated samples divided by 0.57 which is the proportionality factor to convert ammonium to MBN suggested by Moore et al. (2000).

In the second experiment, after removing the resin membranes from the soils, the strips were eluted with 100 mM NaCl/HCl (Kouno et al. 1995), and P was measured using the malachite-green method (Ohno and Zibilske 1991). Other analyses were as described above.

Statistical analysis

In experiment 1, cumulative respiration was analysed by two-way analysis of variance (ANOVA) with fixed factors rewetting time (14 days DRW or constantly moist) and residue treatment (control without residue, barley and faba bean residues).

Data of P pools, resin-P and N, MBN and MBP were analysed by two-way repeated measures ANOVA. The data in experiment 2, data of P adsorbed to the anion exchange membrane and the P pools were analysed by one-way

ANOVA. In experiments 1 and 2, data was log-transformed before running the ANOVA to ensure normality of the data. For each sampling time separately, Tukey's multiple comparison test was used for log-transformed data to determine which treatments were significantly different ($P \geq 0.05$). The statistical analyses were carried out in Genstat v18.2 (VSN International Ltd., UK).

Results

Effect of DRW on microbial activity and P pools in detritusphere of high and low C/P residues (experiment 1)

Respiration rates were lowest in the unamended soil and highest with faba bean where they were two- to fourfold higher than the unamended soil (Fig. 1a–c). Respiration was low in dry soil. Rapid rewetting of dry soil induced a flush of respiration on the first day, followed by a decline on the second day. Respiration rates on day 1 were about twofold higher in rewet soils (RW) than CM. Compared to unamended soil, the flush was about 75% higher with barley and more than twofold higher with faba bean. From day 3 after rewetting onwards, respiration rates were similar to CM. Cumulative respiration from day 0 to day 7 was about twofold higher with faba bean than the control (Fig. 1d). In control and faba bean, cumulative respiration was about 50% higher in RW than CM. Cumulative respiration from day 8 to 14 did not differ between CM and RW (Fig. 1e).

Compared to CM, $CaCl_2$-P, citrate-P, HCl-P, resin-P and available N were higher in dry soil in the control and with barley (Table 2). With faba bean, only citrate-P and HCl-P were higher in dry soil than CM. In contrast, MBP was lower in dry soil than CM in all amendment treatments. Acid phosphomonoesterase-P and MBN did not differ between dry soil and CM. The concentration of most P pools and available N was higher with faba bean than barley or control soils. $CaCl_2$-P, citrate-P and acid phosphomonoesterase-P did not differ between barley and control soils. But HCl-P was higher in the control than with barley. In dry soil, MBP was lowest with faba bean and highest with barley, but MBP in CM was highest with faba bean and lowest in the control. MBN did not differ among the amendment treatments, but available N was highest with faba bean and lowest with barley.

After rewetting, the concentration of all P pools was higher with faba bean than with barley or in the control (Fig. 2). But

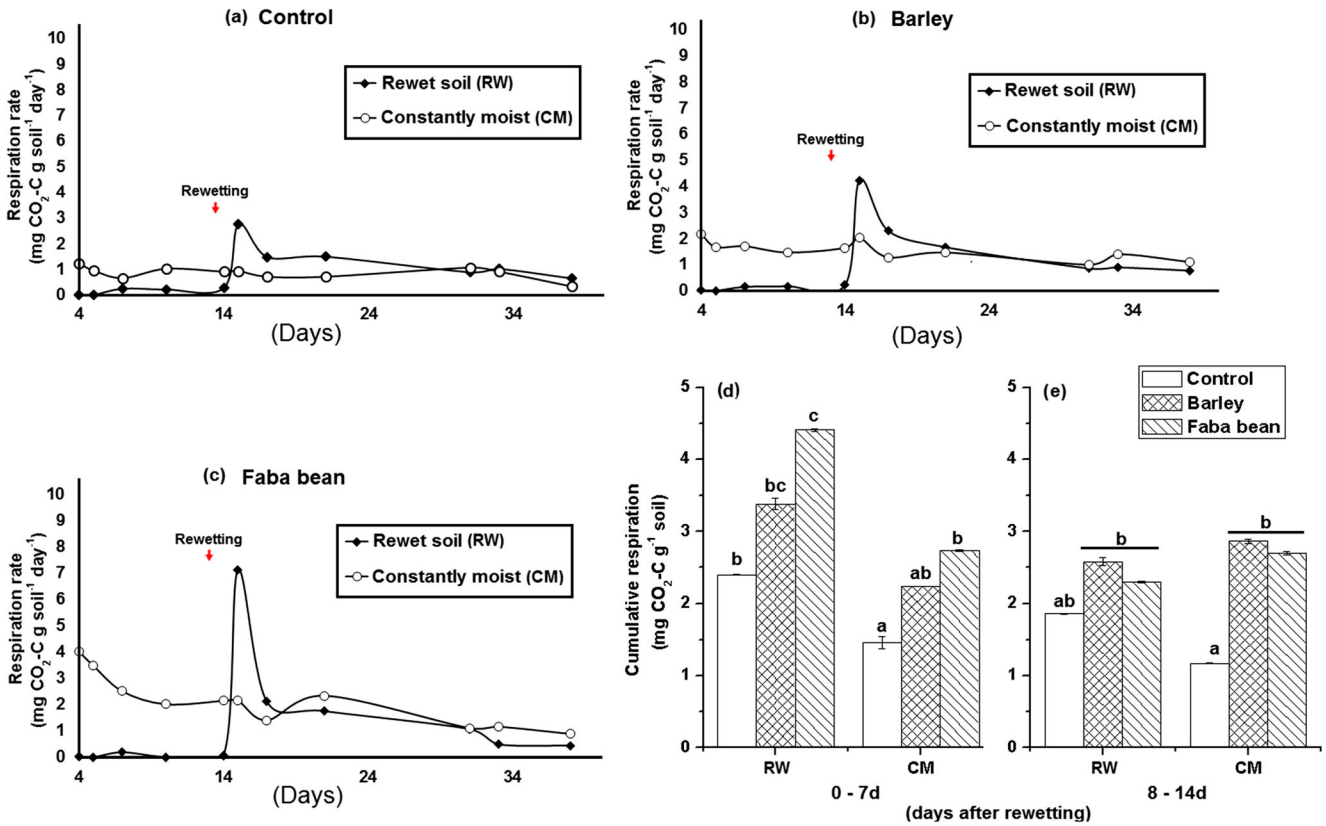

Fig. 1 Respiration rate after rewetting (RW) following a 14-day dry period, or maintained constantly moist (CM) in unamended control (**a**), detritusphere soils of barley (**b**) and faba bean residue (**c**) cumulative respiration (**d**) from day 0 to day 7 and day 8 to 14 after rewetting in control, barley and faba bean detritusphere soils (**e**). Columns in panels **d**, **e** with different letters are significantly different ($P \geq 0.05$, n=4)

Table 2 P pools, microbial biomass N (MBN) and available N in control and detritusphere soils after 14-day dry period and in constantly moist (CM) soil. Means within a column followed by different letters are significantly different ($P \geq 0.05$, $n = 4$)

Residue	Moisture treatment	$CaCl_2$-P	Citrate-P	Acid phosphomonoesterase P	HCl-P (mg kg^{-1})	Microbial biomass P	Resin-P	Microbial biomass N	Available N
Control	Dry	0.16 ± 0.00b	27.99 ± 0.01c	5.33 ± 0.01a	78.21 ± 0.01d	2.97 ± 0.01b	4.60 ± 0.03b	49.36 ± 0.00a	47.75 ± 0.04c
	CM	0.00 ± 0.00a	21.48 ± 0.02b	6.41 ± 0.07a	65.73 ± 0.01b	3.88 ± 0.04c	1.85 ± 0.03a	41.03 ± 0.13a	18.50 ± 0.06a
Barley	Dry	1.88 ± 0.12b	26.79 ± 0.01c	5.45 ± 0.04a	69.08 ± 0.01c	4.62 ± 0.05c	2.05 ± 0.06b	26.31 ± 0.02a	23.24 ± 0.10b
	CM	0.00 ± 0.00a	17.61 ± 0.03a	3.38 ± 0.11a	52.93 ± 0.01a	5.61 ± 0.06d	0.98 ± 0.20a	31.43 ± 0.31a	14.95 ± 0.04a
Faba bean	Dry	43.81 ± 0.00c	332.83 ± 0.00e	200.19 ± 0.01b	371.08 ± 0.00f	1.99 ± 0.01a	87.48 ± 0.00c	47.37 ± 0.00a	263.79 ± 0.09d
	CM	31.50 ± 0.00c	284.50 ± 0.00d	174.63 ± 0.01b	308.16 ± 0.01e	18.52 ± 0.01e	75.95 ± 0.01c	41.42 ± 0.18a	272.39 ± 0.00d

there was no consistent change over time in $CaCl_2$-P, acid phosphomonoesterase-P, citrate and HCl-P.

With faba bean, $CaCl_2$-P did not differ between RW and CM (Fig. 2a). In the control and with barley, 1 day after rewetting, $CaCl_2$-P did not differ between CM and RW or between barley and control soils. Seven days after rewetting, $CaCl_2$-P was tenfold higher in RW than CM in the control and twofold higher with barley. Fourteen days after rewetting, $CaCl_2$-P was about four-fold higher in RW than CM with barley and in the control.

Acid phosphomonoesterase-P did not differ between RW and CM in the control (Fig. 2b). With faba bean it only differed 7 days after rewetting where it was about 30% lower in RW than in CM, and with barley only 14 days after rewetting where it was 75% higher in RW than in CM.

In the control, citrate-P was higher in RW than in CM at all sampling dates, with the greatest difference (75% higher) 1 day after rewetting (Fig. 2c). With barley, citrate-P was higher in RW than CM (20% higher) only 14 days after rewetting. One and 7 days after rewetting, citrate-P was about 15% lower in faba bean RW than in CM. Citrate-P was higher in the control than that in barley except in CM 7 days after rewetting.

HCl-P in the control and with barley was about 10% higher in RW than CM at all sampling times (Fig. 2d). With faba bean, HCl-P was higher in RW than in CM only 7 days after rewetting whereas it was lower in RW 1 and 14 days after rewetting. HCl-P was generally higher in the control than with barley.

Resin-P did not differ between RW and CM in the control and with faba bean (Fig. 2e). With barley, resin-P was lower in RW than CM 7 and 14 days after rewetting. Seven and 14 days after rewetting in RW, resin-P was lower with barley than in the control. There was no difference in MBP between RW and CM 1 and 7 days after rewetting (Fig. 2f). But 14 days after rewetting, MBP with barley and faba bean was nearly twofold higher in RW than in CM. In CM, MBP was higher with barley than the control only 1 day after rewetting. MBP was generally about threefold higher with faba bean than with barley or the control.

Available N did not differ between RW and CM 1 day after rewetting (Fig. 3a). But 7 days after rewetting, it was higher in RW than in CM in detritusphere soils and the control with greater differences in the control and with barley (twofold higher) than with faba bean (25% higher). Two weeks after rewetting available N was 10% higher in RW than CM in the control. But with barley, it was 15% lower in RW than CM. Available N was generally higher with faba bean than with barley and the control. Available N differed little between control and with barley.

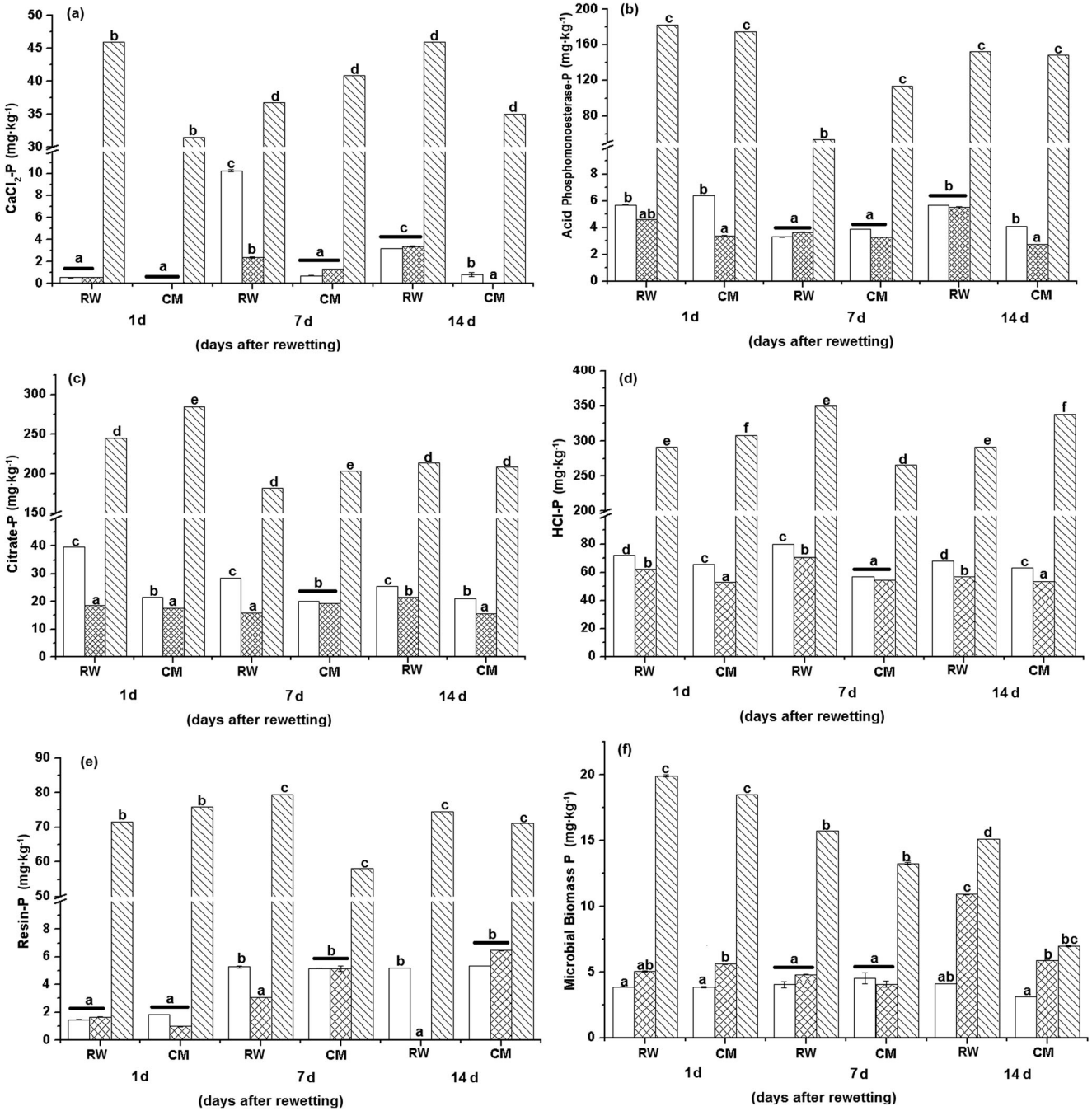

Fig. 2 $CaCl_2$-P (a), acid phosphomonoesterase-P (**b**), citrate-P (**c**), HCl-P (**d**), resin-P (**e**) and microbial biomass P (**f**) in control, barley and faba bean detritusphere soils, 1, 7 and 14 days after rewetting (RW), or in constantly moist (CM) soils. For each sampling time separately, columns with different letters are significantly different ($P \geq 0.05$, $n = 4$)

One day after rewetting, MBN did not differ between CM and RW and was similar in detritusphere soils and the control (Fig. 3b). In the control and with faba bean, moisture treatment also did not affect MBN 7 and 14 days after rewetting. With barley in RW compared to CM, MBN was about 30% lower 7 days after rewetting, but twofold higher after 14 days. MBN was about three to fivefold higher with faba bean than with barley and the control in both CM and RW.

Effect of DRW and P removal by AEM on detritusphere P pools (experiment 2)

The concentration of P adsorbed by the anion exchange membrane (AEM) after contact with the soil was two to more than tenfold higher with faba bean than in the control (Table 3). In the control, there was no difference in P sorbed to AEM between RW and CM and no change over time. With faba bean,

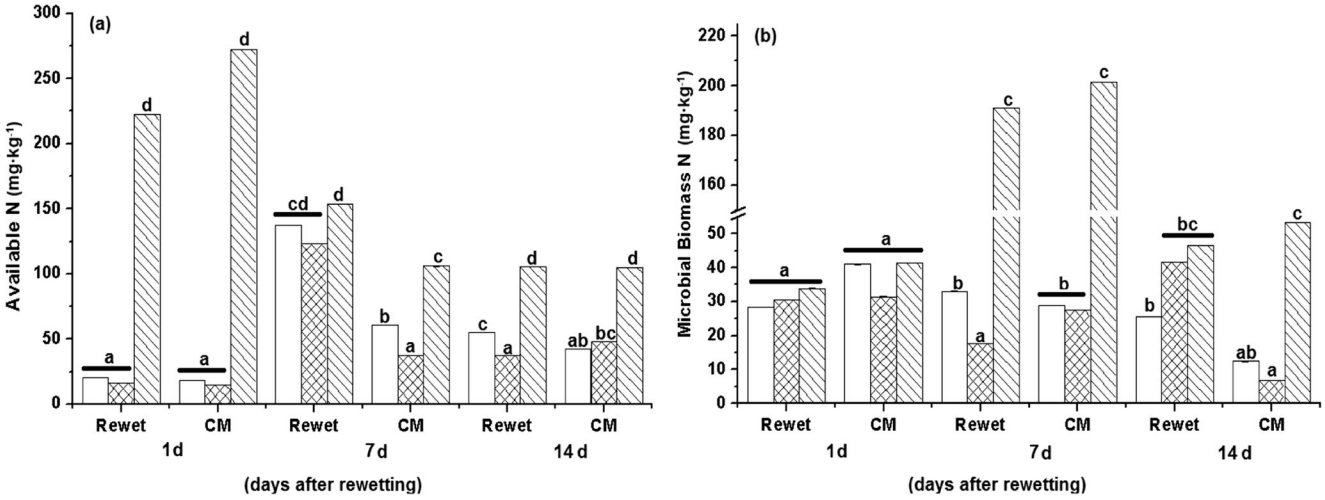

Fig. 3 Available N (**a**) and microbial biomass N (**b**) in control, barley and faba bean detritusphere soils, 1, 7 and 14 days after rewetting (RW), or in constantly moist (CM) soils. For each sampling time separately, columns with different letters are significantly different ($P \geq 0.05$, $n = 4$)

three, four and 2.5-fold more P was adsorbed by AEM in RW than CM after 1, 2 and 4 days, respectively. P sorbed to AEM was about twofold lower on day 4 than day 1.

After 4 days of incubation with AEM, all P pools were higher with faba bean than in the control (Fig. 4). With faba bean, nearly all P pools were 10–30% lower in RW than in CM, except citrate-P which was about 5% higher in RW. In the control, P pools were similar in RW and CM.

P loss from pre-loaded AEM strips (experiment 3)

One day after inserting the P-loaded AEMs in the moist control soil, the concentration of P on the membrane was 25% higher (0.40 mg·kg^{-1}) than after loading (0.30 mg·kg^{-1}) (Fig. 4). Two and 4 days after insertion, the P concentration on the AEM was 4% (0.38 mg kg^{-1}) and 27% (0.28 mg kg^{-1}) lower than day 1, respectively.

Discussion

This study showed that if P is not removed from the soil (experiment 1), P pools are generally little affected by drying and rewetting. However, with removal of P released upon rewetting by AEM, P pools in faba bean detritusphere were lower in RW than CM. This indicates that shortly after rewetting, P is released from all measured P pools which confirms rapid rewetting will induce a transient increase in available P pools compared to constantly moist soils. If P released upon rewetting is not removed from the soil, P is rapidly converted back into less available P pools.

Effect of DRW on microbial activity and P pools in detritusphere of high and low C/P residues (experiment 1)

As was found in previous studies (Gaillard et al. 1999; Liu et al. 2011; Alamgir and Marschner 2016), respiration, P pools and available N were higher in the detritusphere of faba bean which has low C/N and C/P ratios than with barley or in the control. Although residues were removed before using the soil in the experiments, soluble compounds released from the residues during the previous decomposition will be present in the detritusphere soil, particularly that of faba bean. These would provide substrate for microbes in the experiments described here. Additionally, small residue particles (< 0.8 mm) may have fallen through the mesh and served as nutrient source for microbes. It cannot be ruled out that a proportion of the P

Table 3 P concentration of anion exchange membranes in rewet (RW) and constantly moist (CM) detritusphere of faba bean residue or the control after 1, 2 and 4 days soil contact. Means within a column followed by different letters are significantly different ($P \geq 0.05$, $n = 4$)

Residue	Moisture treatment	Days after rewetting		
		1	2	4
		mg P· 3 strips^{-1}		
Control	RW	0.03 ± 0.01a	0.06 ± 0.00a	0.03 ± 0.00a
	CM	0.04 ± 0.01a	0.04 ± 0.00a	0.04 ± 0.01ab
Faba bean	RW	0.45 ± 0.22b	0.41 ± 0.16b	0.21 ± 0.00c
	CM	0.15 ± 0.07a	0.09 ± 0.00a	0.08 ± 0.03b

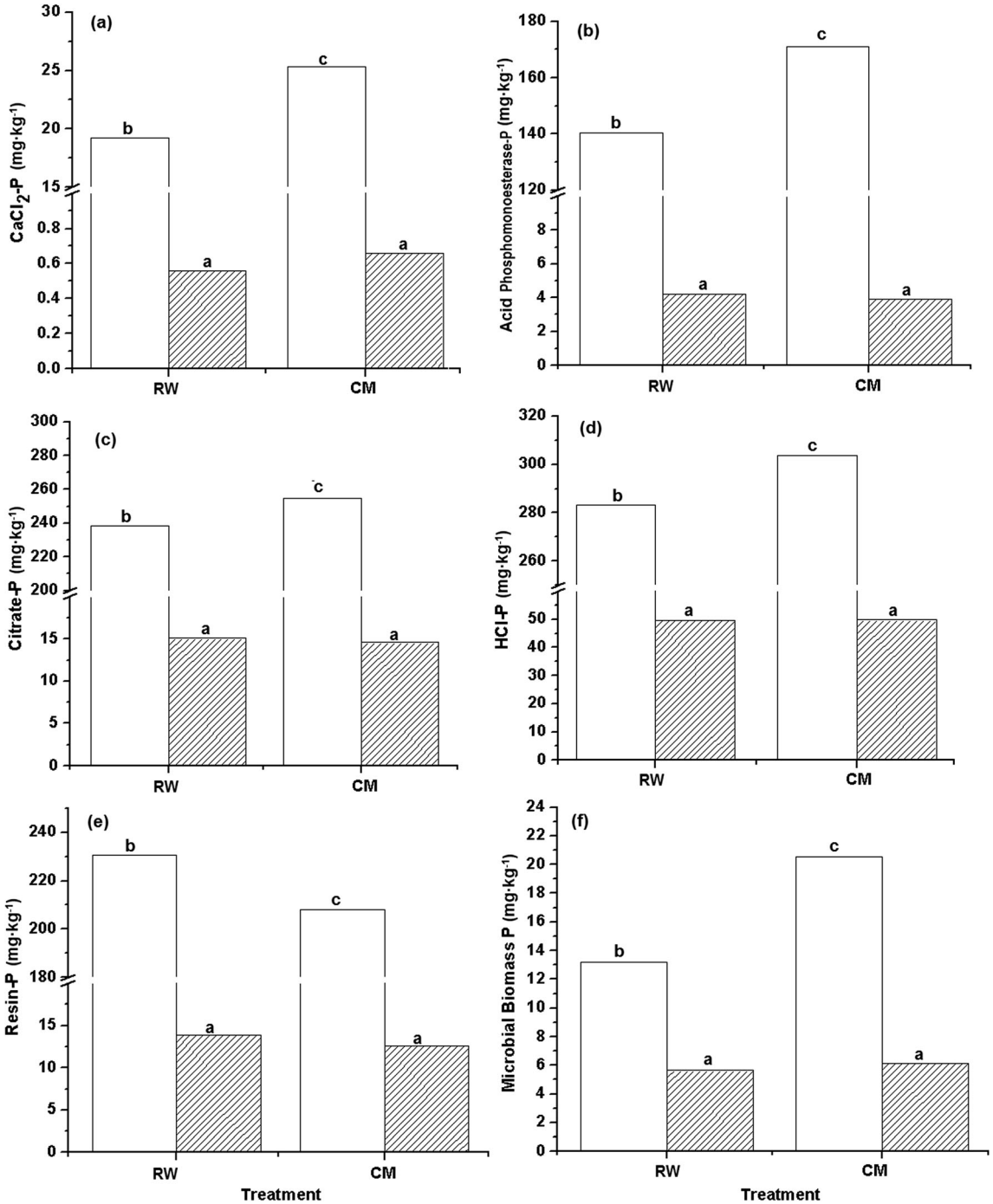

Fig. 4 $CaCl_2$-P (**a**), acid phosphomonoesterase-P (**b**), citrate-P (**c**), HCl-P (**d**), resin-P (**e**) and microbial biomass (**f**) P in control soil ☐ and faba bean ▨ detritusphere and, 4 days after rewetting (RW), or in constantly moist (CM) soils after placement of resin strips for 4 days. Columns with different letters are significantly different from one another ($P \geq 0.05$, $n = 4$)

was extracted from such residue particles, but we assume that this proportion is small because only few residue particles are likely to have fallen through the fine mesh.

Most P pools and available N were similar with barley and the control. Due to its high C/N and C/P ratio, it could be expected that barley induced net N and P immobilisation (Jensen 1997; Kabba and Aulakh 2004; Alamgir et al. 2012). This may have also occurred in the first 14 days during which the detritusphere was generated. By the time the soil was used for the experiments, microbial biomass turnover may have released previously immobilised P.

Substrate supply to microbes is restricted in dry soil (Steiner 1994; Homyak et al. 2016), which can explain the lower respiration and MBP compared to moist soil. In contrast

to MBP, MBN was not influenced by soil water content which indicates that in dry soil, P supply to microbes is more restricted than N supply. Microbes may have been able to take up sufficient N as the soils dried, but little P. In dry compared to moist soil, readily available P pools ($CaCl_2$- and resin-P) and P bound to soil particles (citrate and HCl-P) were higher. The higher readily available P may be an artefact of the extractants used to determine the pools. In dry soil, addition of the extractant resembles rewetting of dry soil which may induce the release of P. This could also explain the higher available N in dry soil of the control and with barley. Soil moisture did not influence available N with faba bean, probably due to the very high N availability, even in dry soil. The addition of extractant to dry soil may also contribute to the higher citrate- and HCl-P. However, these P pools may be higher in dry than moist soil because P has been shown to be more strongly bound to soil particles in dry soil (Bartlett and James 1980; McBeath et al. 2012).

In agreement with previous studies (Butterly et al. 2011; Manzoni et al. 2012; Shi and Marschner 2015), rewetting of dry soil induced a flush of respiration where the respiration rate 1 day after rewetting was twofold higher than in CM. The rewetting flush has been explained by increased substrate availability to surviving microbes due to death of sensitive microbes, release of osmolytes and exposure of previously occluded organic matter (Borken and Matzner 2009). The flush upon rewetting resulted in higher cumulative respiration in the first week. By the second week, respiration was similar in CM and RW indicating depletion of substrates that had been released after rewetting.

P pools were largely unaffected by water regime and remained stable over time after rewetting, but were strongly influenced by residue type (barley and faba bean residues). The stronger effect of P supply on P pools than soil water content is in agreement with Sun et al. (2018). They found that the P source (mineral and manure treatments) was more important than water regime in determining the labile P pools (microbial biomass, and acid phosphomonoesterase-P). In our study, P may have changed from one pool to another during the experiment, e.g. $CaCl_2$-P to citrate-P, but this appears to have been compensated by P fluxes from other pools. With faba bean 1 day after rewetting, resin-, citrate- and HCl-P were lower in dry soil whereas MBP was higher. This suggests that at high concentrations of these pools as with faba bean, P is released upon rewetting, some of which was immobilised by soil microbes. Yevdokimov et al. (2016) reported strong microbial immobilisation (up to 41%) of ^{33}P after rewetting an air-dried soil. The lower citrate- and HCl-P in RW compared to CM 1 day after rewetting suggests that P was released from these pools. It is also possible that rewetting induced formation of P pools not assessed by the DeLuca method such as P very strongly bound to soil particles or Fe/Al oxides. In the control on the other hand, citrate 1 day after rewetting was higher in RW than CM. This indicates that when small amounts of P are released upon rewetting, P is sorbed to soil particles, but remains extractable by citrate and HCl.

Seven and 14 days after rewetting, HCl-P in the control and with barley was higher in RW than in CM which was also the case for citrate-P in the control. This was not due to release of P from any of the other measured P pools which suggests that P was released from forms that are not assessed by this extraction method, e.g. native organic matter. The latter is supported by the higher soil respiration in the first 7 days after rewetting compared to CM indicating enhanced decomposition. With barley, mineralised P was taken up by the soil microflora, but not in the control which can be explained by the greater substrate supply in barley detritusphere soil.

As mentioned above, previous studies reported an increase in available P upon rewetting (Butterly et al. 2011; Bünemann et al. 2013). However in experiment 1, available P pools ($CaCl_2$- and resin-P) 1 day after rewetting were similar in RW and CM. It is possible that P had been released immediately after rewetting, but after 1 day, had been sorbed to soil particles, i.e. citrate- and HCl-P. Butterly et al. (2011) found that available P was higher in RW than in CM 1 h after rewetting, but was not affected by moisture treatment 7 days after rewetting.

Effect of DRW and P removal by AEM on detritusphere P pools (experiment 2)

To determine if P was released upon rewetting in the detritusphere, we conducted the second experiment where AEM were placed in the dry soil from faba bean detritusphere and an unamended control before the soil was rewetted. The higher P concentration on AEM of RW than CM of faba bean indicates that P was released into the soil solution upon rewetting. This is in agreement with other studies and confirms the influence of rewetting on available P when P pools are large, i.e. in the detritusphere of low C/P residue. Without removal from the soil solution, the released P is rapidly sorbed to soil particles, making the window for P uptake by roots or microbes very short. Therefore, the first hypothesis (rapid rewetting will induce a transient increase in available P pools compared to constantly moist soils, but have little effect on more stable soil P pools), and second hypothesis (the influence of rewetting on available P will increase in the following order control < detritusphere soil of high C/P < low C/P residue) can be accepted.

P desorption from pre-loaded AEM strip (experiment 3)

The P concentration on AEM in experiment 2 was highest on the first day after rewetting which suggests that P was released immediately after rewetting. The decrease in P concentration

on AEM after 4 days contact with the soil can be explained by desorption of P from AEM which was confirmed in the third experiment, where AEM were loaded with P and then placed into the soil. Approximately 30% of P was lost from AEM after 4 days. P on AEM is in equilibrium with the soil solution. In the days following the initial P release upon rewetting in faba bean detritusphere and control soil (experiment 2) and in constantly moist soil (experiment 3), the P concentration in the soil solution is likely to be lower than on the AEM due to P sorption to soil particles. This would induce release of P from the AEM.

Conclusion

If labile P (extractable by anion exchange resin) is not removed from soil, rewetting had little effect on P pools although rewetting induced a transient increase of P in the soil solution. However, if P released at rewetting is removed from soil with high P concentration such as in the detritusphere of faba bean, P pools were lower in rewet compared to constantly moist soil. This suggests that in the field where plants may take up P released at rewetting, repeated dry-rewetting events may gradually deplete P pools compared to constantly moist soil.

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