THE UNIVERSITY OF ADELAIDE

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EFFECT OF CROP RESIDUE QUALITY ON PHOSPHORUS POOLS IN THE DETRITUSPHERE AND P UPTAKE BY WHEAT

Thesis submitted to the University of Adelaide in fulfilment of the requirements for the degree of Doctor of Philosophy

School of Agriculture, Food and Wine

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Abstract

Little is known about the effect of the influence of water availability, crop residue quality and plant growth on phosphorus (P) pools in the detritusphere, the soil adjacent to plant residues. The detritusphere soil was generated in microcosms as described in Ha et al. (2007). The soil at 0-2 mm distance from the surface of soil incubated in PVC caps was collected as the detritusphere soil and used for further experiments. Bioavailable P pools (readily available P pools: $CaCl_2$ and anion exchange P; P bound to soil particles: citrate and HCl P; acid phosphatase and microbial P), available N and microbial N were measured in the detritusphere.

The experiment described in Chapter 2 investigated the influence of drying and rewetting on soil P pools in the detritusphere of two crop residues, young faba bean residue (C/P 38) and mature barley straw (C/P 255). The detritusphere and unamended control soils were dried to approximately 5% water holding capacity (WHC) and kept dry for two weeks followed by rapid rewetting to 50% WHC, or maintained at 50% of WHC. Rewetting of dry soils induced a respiration flush and the flush was greater with faba bean than barley. P pools were higher with faba bean than with barley, due to lower C/P ratio of the former. In general, drying and rewetting had little effect on P pools.

In Chapter 3, an experiment is described that assessed the influence of soil water availability on P pools in the detritusphere of crop residues. Detritusphere was generated with barley straw (C/P 255) or barley straw mixed with faba bean residue at a 75:25 ratio (C/P 200) in soil at 50% WHC. Water availability in the detritusphere soils was reduced to -0.320 and -1.700 MPa (30% and 10% WHC), or maintained at -0.078 MPa (50% WHC). In the detritusphere of the residue mix, soil respiration, P pools and available N were lower at -1.700 MPa than at -0.078 MPa. However, water availability had little effect in barley detritusphere.

The aim of the experiment described in Chapter 4 was to elucidate the effect of soil amendment with inorganic N and P on P pools in the detritusphere of mature barley straw (C/N 95; C/P 255). Addition of inorganic N to soil increased P pools likely due to enhanced mineralisation of native soil organic matter. Barley straw decomposition reduced available P pools in the detritusphere, particularly in soil to which inorganic P was added.

In Chapter 5, an experiment was described to determine the influence of a change of residue types on P pools in the detritusphere of crop residues with differing C/P ratios. In the first experiment, after two weeks of incubation at 50% WHC, with young faba bean residue (L) or mature barley straw (H), the residues were replaced with either a H or L, resulting in four residue treatments: high-high (HH), high-low (HL), low-low (LL) or low-high (LH), which

were incubated for another 14 days. On day 14, P pools and available N were higher, but MBP and MBN were lower in L than in H. On day 28, P pools and available N followed the order LL>HL>LH>HH, whereas MBN and MBP were highest in HL.

The experiment described in Chapter 6 aimed to determine the influence of residue C/P ratio on changes in P pools and N availability in wheat rhizosphere. Pre-germinated wheat seeds were sown in unamended soil or soil amended with two crop residues (young faba bean residue, C/P 38; mature barley straw, C/P 255). After 28 days with faba bean, P uptake in wheat was higher than with barley straw and control. P pools were lower in the interface of wheat rhizosphere and faba bean detritusphere than in detritusphere alone, due to plant uptake. With barley straw, presence of wheat roots had no effect on P pools.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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List of publications arising from this thesis

1. **Erinle K. O.**, Li J., Doolette A., Marschner P. (2018). Soil phosphorus pools in the detritusphere of plant residues with different C/P ratio - influence of drying and rewetting. *Biology and Fertility of Soil*, 54: 841-852.

2. **Erinle K. O.** and Marschner P. (2019). Soil water availability influences P pools in the detritusphere of crop residues with different C/P ratios. *Journal of Soil Science and Plant Nutrition*, 19(4): 771-779.

3. **Erinle K. O.**, Doolette A., Marschner P. (2019). P pools in barley detritusphere are influenced by N and P addition to the soil. *Journal of Soil Science and Plant Nutrition*, 19(2): 463-468**.**

4. **Erinle K. O.**, Doolette A., Marschner P. (2019). Changes in phosphorus pools in the detritusphere induced by removal of P or switch of residues with low and high C/P ratio. *Biology and Fertility of Soil* (doi: https://doi.org/10.1007/s00374-019-01396-1).

5. **Erinle K. O.,** Marschner P. (2019). Wheat growth induced changes in phosphorus pools in the detritusphere of crop residues with low and high C/P ratio. **Submitted to Geoderma.**

Structure of this thesis

The thesis includes 7 chapters and is presented as papers that have been published, or have been submitted for publication.

Chapter 1 provides an overview of soil P pools, factors influencing P pools and transformations and organic amendments.

Chapter 2 is a paper published in *Biology and Fertility of Soil*. It describes the influence of drying and rewetting on soil P pools in the detritusphere of crop residues with different C/P ratio.

Chapter 3 is a paper published in the *Journal of Soil Science and Plant Nutrition*. It assesses the influence of soil water availability on P pools in the detritusphere of crop residues with different C/P ratio.

Chapter 4 is a paper published in the *Journal of Soil Science and Plant Nutrition*. It describes the influence of N and P addition on soil P pools in barley detritusphere.

Chapter 5 is a paper published in *Biology and Fertility of Soil*. It assesses the changes in P pools in the crop residues detritusphere due to P removal or residue switch.

Chapter 6 is a paper submitted for publication in *Geoderma*. It describes the influence of wheat growth on changes in P pools in the detritusphere of crop residues with different C/P ratio.

Chapter 7 includes general conclusions from all chapters and future research suggestions.

Chapter 1. Introduction and review of literature

1.1 Introduction

Phosphorus (P) is the second most important nutrient after nitrogen for all living organisms. It is an essential component for organic compounds such as adenosine triphosphate (ATP), deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and phospholipids which play key roles in energy metabolism, storage and transference of genetic information and as structural components in the cell (Lavelle and Spain, 2002). Total P concentration in soils ranges from 100 to 3 000 mg kg^{-1}, but only a fraction, often less than 0.1%, is immediately available to plants (Frossard et al., 2000; Randriamanantsoa et al., 2015), due to the conversion of available P to various less available pools in the soil. Plants take up P from the soil solution (Schachtman et al., 1998), thereby decreasing the soil solution P concentration and inducing diffusion of P from the surrounding soil. However, a number of soil factors limit P diffusion, thus reducing P availability to plant roots. These include soil water content, soil bulk density, and P sorption capacity of Fe and Al-oxides and hydroxides (Fink et al., 2016).

Addition of crop residues has been shown to improve soil P availability, which could be an important source of P for crops. Depending on the C/P ratio of the added crop residue, soil P availability and other P pools may be affected. For example, addition of crop residues with C/P > 200 will induce a net P immobilization and depletion of soil P pools, whereas addition of crop residues with lower C/P ratio will increase P availability and soil P pools (Dalal, 1979; Umrit and Friesen, 1994; Alamgir et al., 2012). The increase in soil P availability during the decomposition of crop residues could be due to (i) release of P from the residue, and (ii) exchange of organic acid anions produced during residue decomposition with P sorbed on clay particles, and formation of complexes with metals which enhances the dissolution of phosphate compounds (Bolan et al., 1994).

After harvesting and/or before the next cropping season, crop residues may either be left to decompose on the soil surface or incorporated into the soil. Detritusphere refers to the soil that is directly adjacent to decomposing crop residue (≤ 5 mm) which is influenced by residue decomposition (Liu et al., 2011). Compared to the bulk soil, the detritusphere is usually characterized by high concentrations of easily available compounds released from the crop residue (Poll et al., 2010), increased carbon (C) and nitrogen turnover (Kandeler et al., 1999) and higher abundance soil microbes (Marschner et al., 2012). Wang et al. (2016b) suggested that increased C mineralization could increase P release by increasing the mineralization of

organic P. However, P availability and P pools in the detritusphere of decomposing crop residues have not been well studied.

In addition, little is known about the effect of other factors such as soil water availability and roots on P availability and P pools in detritusphere of decomposing crop residues. Therefore, this study was conducted to elucidate the effect of soil water availability, drying-rewetting cycles, and wheat growth on P availability and the P pools in detritusphere of crop residues differing in C/P ratios. The literature review will provide an overview of soil P pools, factors influencing P pools and transformations and organic amendments.

1.2 Phosphorus in soil

There are different inorganic (Pi) and organic (Po) P pools in the soil. Their solubility and availability depends on soil physical and chemical properties (Holford, 1997) and soil management (Sheklabadi et al., 2014). Pi can be in solution or sorbed to Fe and Al oxides. Depending on the extent of sorption, *labile* (weakly sorbed) or *moderately labile* (strongly sorbed) P fractions are formed. When Pi forms salts with Al, Fe and Ca, it may become *non-labile,* depending on the solubility of salt formed. In Po, on the other hand, P is bonded to carbon moieties, and Po lability depends on the decomposability of the organic moiety to which P is bound (Richardson, 2001; Condron et al., 2005; Alamgir and Marschner, 2013a; Costa et al., 2016). Separation of P pools is often based on the Hedley fractionation, which uses various extraction solutions to release P.

Phosphorus fractionation by the Hedley et al. (1982) method has been widely used to determine different P pools. This method separates P pools using a sequence of extractants (bicarbonate, NaOH and acids), into labile P (resin-Pi, $NaHCO_3$-Pi, and $NaHCO_3$-Po), moderately labile (NaOH-Pi, NaOH-Po), and non-labile P (HCl-P and residual Pi in primary minerals) pools. Thus, P pools are characterised based on their susceptibility or resistance to certain chemical extractants (Bowman and Cole, 1978). However, the method has a number of limitations. For example, NaOH is thought to remove P bound to the surface of Fe and Al minerals that can be quite stable (Chang and Jackson, 1957; Levy and Schlesinger, 1999). The fractionation method is time-consuming and requires careful preparation and processing, which makes it unsuitable for routine use, especially in agriculture. Most significantly, the Hedley fractionation method does not adequately reflect rhizosphere processes, as discussed by Johnson et al. (2003) and Yang and Post (2011).

A novel biologically based approach to the evaluation of soil P was developed by DeLuca et al. (2015). The approach utilises a suite of established extraction methods to characterize P pools available via plant and microbial P acquisition mechanisms: (1) 10 mM $CaCl_2$ to extract

immediately available P (soluble P); (2) 10 mM citric acid to extract P that can be complexed by organic acid (chelate extractable P); (3) phytase or phosphatase solution to extract enzyme hydrolysable P (enzyme extractable organic P); and (4) 1 M HCl to extract mineral occluded P. Organic acid anions released by plant roots (Mariano et al., 2005) and during organic matter decomposition (Ritchie and Dolling, 1985) mobilise P through anion exchange and dissolution of Fe and Al, thereby releasing P and reducing the number of P binding sites (Wang et al., 2008; Gang et al., 2012). The advantage of this method compared to the Hedley method is that the extractions are carried out in parallel to determine the total amount of P mobilised by individual extractant. Although the Deluca method is biologically based, it does not include the microbial biomass P, which is a biologically significant soil P pool. Also, commercially available enzyme solutions may be contaminated with P, especially the phytase enzyme solution, thus limiting the method to the use of only one enzyme – phosphatase (DeLuca et al. 2015). Moreover, Clarholm et al. (2015) noted that organic acids and phosphatases are most effective when used in series. Low molecular mass organic acids, e.g. citrate, may destabilize soil organic matter to release dissolved organic matter which is then more likely to be mineralised by phosphatase than without prior treatment with organic acids (Clarholm et al., 2015). Nevertheless, the DeLuca method is useful to determine P pools that are more likely to be relevant for P uptake by plants and microbes than some of the P pools measured by the Hedley fractionation.

First developed by Newman and Tate (1980), ^{31}P nuclear magnetic resonance spectroscopy (^{31}P-NMR) was used to estimate labile and moderately labile organic P pools in New Zealand soils (Zhang, 1996). ^{31}P-NMR technique has two approaches, liquid-state and solid-state. In the liquid-state approach, soil is extracted with a mixture of NaOH and ethylenediamine-tetraacetic acid (EDTA) (Cade-Menun and Preston, 1996; Turner et al., 2003). The extract is then analysed by ^{31}P-NMR. The solid-state approach involves first drying and then grinding the soil (Cade-Menun, 2005). The ^{31}P-NMR technique is used to characterize organic and inorganic P pools, which include orthophosphate monoesters, polyphosphates, orthophosphate and orthophosphate diester. However, despite its versatility, there are a number of disadvantages in the use of ^{31}P -NMR. Firstly, in liquid state NMR, any P that is not solubilized in the extractant will not be measured. Secondly, organic P in solution may be hydrolysed under strong alkaline conditions (Richardson and Simpson, 2011). Thirdly, the ability to interpret the NMR spectra is crucial for correct results. But in many studies peaks are assigned to different P compounds based on values reported in the literature (McDowell et al., 2006; Noack, 2014). This may lead to incorrect assignment of peaks and quantification of P forms.

1.3 Soil phosphorus pools and fluxes

1.3.1 Labile P pools

Labile P pools are assumed to represent potentially available P (Reddy et al., 1999; Saleque et al., 2004; Malik et al., 2012). Labile P pools comprise resin Pi, $NaHCO_3$ Pi and $NaHCO_3$ Po. At high soluble P concentration, P can be sorbed to Al and Fe oxides or clay minerals (Sample et al., 1980; Razaq, 1989). Soluble P is also taken up by soil microorganisms for growth of the microbial biomass (McLaughlin et al., 1988). Microbial biomass can release P upon turnover thus forming a labile P pool. Over time, labile P can change into less labile P pools.

1.3.2 Moderately labile pools

The moderately labile pool is NaOH-extractable P (Hedley et al., 1982). Moderately labile P pools can, with time and as a result of various reactions in the soil, be transformed to the labile P pools. As noted by Beck and Sanchez (1994), the NaOH-extractable Po pool can replenish plant available P (labile P pool) by mineralization. Zheng et al. (2002) reported transformation of NaOH-Po to labile Pi pools (resin-P, $NaHCO_3$-Pi) in dairy manure. Hinsinger and Gilkes (1996) found that NaOH-P was depleted in the rhizosphere of ryegrass. This could be due to NaOH-Po mineralisation as the amount of P taken up by the ryegrass closely matched NaOH-Po depletion. The increase in available P could also be due to interactions between P ions and root exudates. Root exudates such as organic acid anions, compete with P sorbed onto metal oxides (Hinsinger, 2001), resulting in release of P into soil solution.

1.3.3 Non-labile pools

Non-labile P includes Pi and Po in hydroxide, Pi in HCl and residual P (Cross and Schlesinger, 1995; Costa et al., 2016). The residual P pool may be involved in long-term P availability (Ball-Coelho et al., 1993). According to Braos et al. (2015), non-labile organic P is the sum of humic acid Po and residual Po, and not affected in the short term by soil management and fertilizer application (Gatiboni et al., 2007). Agbenin and Goladi (1998) reported that application of inorganic P fertilizer increased HCl-P (Ca-bound P) by about 69%, but residual P was reduced by 43%, compared to the unfertilized control. The decrease in residual P reported by Agbenin and Goladi (1998) could be through mineralisation of soil organic matter.

Transformations of P among the various pools discussed above depend on the interactions among plants, soil microbes, soil particles and organic matter through processes such as immobilization-mineralization, precipitation, solubilisation, and sorption-desorption (Stewart and Tiessen, 1987; Iqbal, 2009) (Fig. 1.1 and Fig. 1.2).

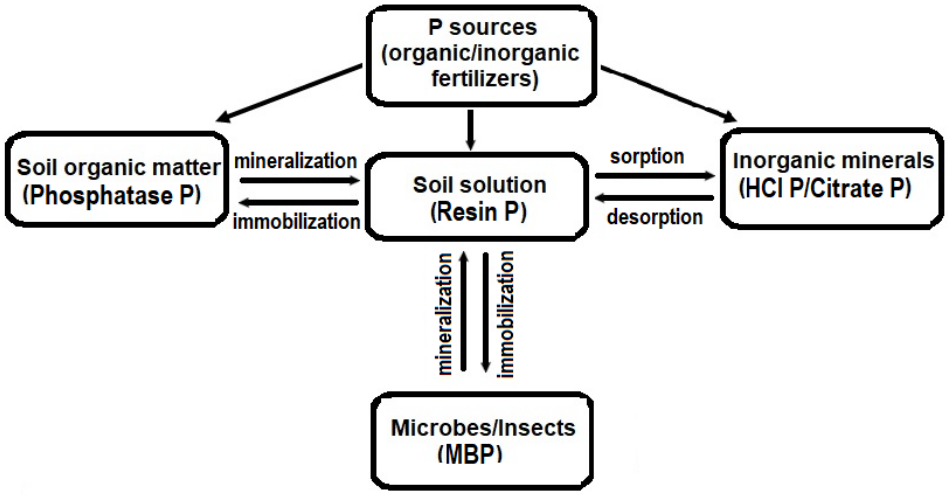

Figure 1.1. Soil P pools extracted by the Deluca method (Deluca et al., 2015) and their interactions

When inorganic P is added to soil, Pi is released into the soil solution and is readily available to plant roots or for microbial uptake (labile P) (Schachtman et al., 1998). *Immobilization* of P occurs by microbial uptake and incorporation into the microbial biomass (McLaughlin et al., 1988). *Mineralization*, which is the decomposition of organic materials, is responsible for the release of P 'locked-up' in organic materials as Po (moderately labile P) and conversion into inorganic P. Mineralisation is catalysed by enzymes such as phosphatases, phytases and/or phosphonases. Inorganic P *solubilisation* can be due to root exudates or soil microorganisms such as phosphate solubilizing microbes, which release inorganic P as orthophosphate from poorly soluble inorganic P forms (Ahmed and Shahab, 2011). P solubilisation may either be the result of pH change or organic acid production (Illmer and Schinner, 1995; Puente et al., 2004). According to Razaq (1989), *sorption* occurs through fixation of P by Al and Fe oxides and clay minerals (Sample et al., 1980; Razaq, 1989), especially at low soil solution pH. P *precipitation*, on the other hand, involves the formation of insoluble mineral complexes (Ca-P, Al-P, and Fe-P.) with cations like Fe^{3+} and Al^{3+} in acid soils and with Ca^{2+} in alkaline soils (Tunesi et al., 1999).

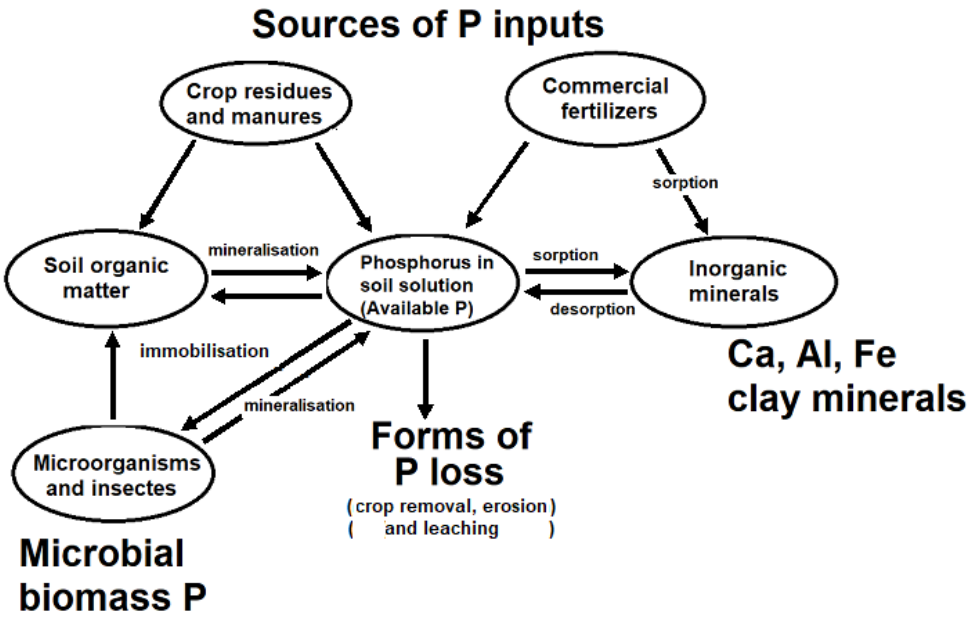

Figure 1.2. Soil P cycle (http://farmingnomad.blogspot.com.au/2012/10/phosphorus.html)

Sorbed P is released by desorption which is more rapid (moderately labile) than solubilisation of precipitated P (non-labile) (Sharpley et al., 1992). As noted by Zhang (1996), sorption-desorption processes control the release of P for crops. Labile and moderately labile P can change to residual P (non-labile P). Reaction of P and Al/Fe hydrous oxides in the soil, precipitation with Ca, Fe or Al or immobilization of inorganic P in organic matter convert labile P to non-labile P (Braos et al., 2015).

1.4 Environmental factors affecting P pools and fluxes

The fate of P in the soil is governed by a number of factors such as soil pH, initial P concentration in the soil, microbial activity, temperature, soil water content and clay content (Blair and Boland, 1978).

1.4.1 Soil pH

Phosphorus in the soil solution is in the form of orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}) (Becquer et al., 2014). The ratio of these two forms is determined by the pH of the soil solution, with $H_2PO_4^-$ predominant in acidic soil, and HPO_4^{2-} dominating in alkaline soil (Menzies, 2009; Oka, 2015). Below pH 5.5, there is a net increase in positive charge on the surface of colloids, which is due to increased protonation. This increases the affinity of Fe and Al ions often associated with soil particles (Siebielec et al., 2015) for P, consequently increasing P sorption (Hinsinger, 2001). In acidic soils, P sorption can be reduced by liming Murrmann and Peech (1969). At pH between 5.5 and 7.5, P in the soil solution increases (Lindsay, 1979; Razaq, 1989) because P sorption by hydroxyl Fe and Al surfaces decreases with increasing pH (Juo

and Fox, 1977; Kwong et al., 1979; Bowden et al., 1980). Haynes (1982) further explained that increasing pH caused greater electrostatic repulsion and hence decreased electrostatic potential. This lowers the positive charge of Fe and Al (hydr)oxides on colloidal surfaces, thereby reducing P sorption and releasing P into the soil solution. A pH increase can also increase the cation exchange capacity (CEC) by formation of negative charges on soil particles (Iyamuremye et al., 1996). The increased negative charge or CEC results in increased sorption of cations such as Fe and Al which can bind P. Mashal et al. (2011) found that CEC and Al/Fe-oxide were the two most significant predictors of P availability and occurrence in calcareous soils. Similarly, Mahmood et al. (2000) noted that P sorption was positively correlated with CEC, clay content and soil pH.

1.4.2 Temperature

Soil temperature, water content and substrate availability are the major environmental factors controlling soil microbial activity (Iovieno and Bååth, 2008). Organic matter is broken down by soil microorganisms to release Po which is further mineralized into available P. Temperature is an important factor for microbial transformations. When water is not limiting, the optimum temperature for bacterial growth is between 30-40 ^{o}C (Stanier et al., 1971). Acquaye (1963) reported highest organic P mineralization in soils at 50% of maximun water holding capacity and 50^{o}C. Also, Thompson et al. (1954) recorded higher organic P mineralization at 50^{o}C than at 35^{o}C. On the other hand, Gaind and Gaur (1991) observed maximum phosphate solubilisation by phosphate solubilizing microorganisms at 45 ^{o}C, and Panda et al. (2013) recorded highest P solubilisation by *Pseudomonas fluorescens* at 35 ^{o}C. Temperature can also increase the rate of reaction between soil particles and added P, resulting in a rapid decrease in soluble P. Generally, P sorption increases with rising soil temperature. As described by Barrow (1974), the increase in P sorption occurs as a result of migration of P ions into micropores of soil aggregates and soil mineral structures, which decreases the concentration of soluble P (Barrow and Shaw, 1975; Sah and Mikkelsen, 1986).

1.4.3 Soil water content

Increasing soil water content increases the diffusivity of P, thereby enhancing P uptake by plants and microbes (Lambers et al., 2006). On the other hand, low soil water content can decrease P uptake by reducing diffusion in the soil (Chapin III, 1991; Lambers et al., 2006; He and Dijkstra, 2014).

Soil water content, apart from temperature, determines size and activity of the microbial biomass and causes seasonal changes in microbial activity (Chen et al., 2003). He et al. (1997) reported a decrease in microbial biomass P by 22-64% over a dry summer. This is likely due to

low microbial activity because solute and enzyme mobility decrease with soil water content (Manzoni et al., 2012), thus limiting substrate supply to the decomposers (Skopp et al., 1990; Or et al., 2007; Manzoni et al., 2012).

(a) Water potential and water availability

Water flows from high to low energy. Therefore, water moves from a zone of high free energy (standing water table) to a zone of low free energy (dry soil) (Cook and Papendick, 1972). The soil water retention curve (also referred to as soil water characteristics curve) expresses the soil water content based on its energy state or potential (Reichert et al., 2009). For example, water retained at -33 kPa is defined as field capacity and that at -1,500 kPa as permanent wilting point; water retained between -33 and -1,500 kPa is defined as plant available water. Water is held in soil pores and interconnecting pore necks by matric potential, which results from capillarity and adhesive forces of soil particles (Derjaguin et al., 1987; Lu and Likos, 2004). In saturated soil, all pores are filled with water and the hydrostatic pressure is greater than atmospheric pressure; water tends to move from the soil to the free water surface. In saturated soil, the soil water potential is positive (Hillel, 2013). As the soil dries, water is lost first from the larger pores due to a low adhesive force between water and soil particles in larger pores. The matric potential becomes increasingly negative as water is held more tightly in smaller pores. Then, water movement is controlled by capillarity and adhesive forces and the hydrostatic pressure is less than the reference point (free water surface) (Hillel, 2013). Negative matric potential means that it takes energy to remove water from the soil (Beckett and Augarde, 2013).

As described by Wolf et al. (2013), the water content of a soil at a given matric potential depends on the distribution of the pore sizes (diameters). The pore size distribution of a soil can be determined from the water retention curve (Danielson and Sutherland, 1986). Li and Chen (2016) described that the soil water retention curve (Fig. 1.2) plays an important role in understanding processes in unsaturated soils (Fredlund et al., 1996; Ajdari et al., 2012). The water retention curve is affected by factors such as temperature (Peck, 1960; Wilkinson and Klute, 1962; Chahal, 1965), particle-size distribution (Yang et al., 2004; Chiu et al., 2012) and thus soil texture (Hillel, 2013) and bulk density (Zhou et al., 2014). In a clay soil, water retention is greater at any particular matric potential than in coarser textured soils (Fig. 1.3). More water is held due to the high proportion of small pores. Thus, an increase in matric potential will cause a more gradual decrease in water content than in a sandy soil (Zhan and Ng, 2004). In sandy soil due to the larger pore sizes, water is rapidly drained; at a given water potential a smaller amount of water remains than in a clay soil (Zhan and Ng, 2004; Hillel, 2013). A strong

reduction in water content in sandy soil will result in a sharp decrease of water permeability with increasing water potential (Zhan and Ng, 2004).

Soil drying after wetting is due to evapo-transpiration or infiltration (Ojeda and Alcañiz, 2010). As the soil dries, the water potential becomes more negative (Cook and Papendick, 1972). Water uptake by roots or microbes is inhibited if soil water potential is more negative than that to which cells can adjust their water potentials (Ungar, 1977). Furthermore, nutrient availability becomes a constraint at low water content. Watanabe et al. (1960) found that maximum P availability for most crops was at about -33 kPa (that is, field capacity). This is in agreement with the study of Bacon and Davey (1982) who reported a rapid decrease in available P as soil water content decreased below field capacity. According to Barber (1980), the volume of water in the soil has a significant effect on the cross-sectional area through which P can diffuse. Hence, as the soil dries, the path of P diffusion in the soil becomes more tortuous, consequently increasing path length and the likelihood of P coming in contact with the soil particles that render P insoluble (Barker and Pilbeam, 2015).

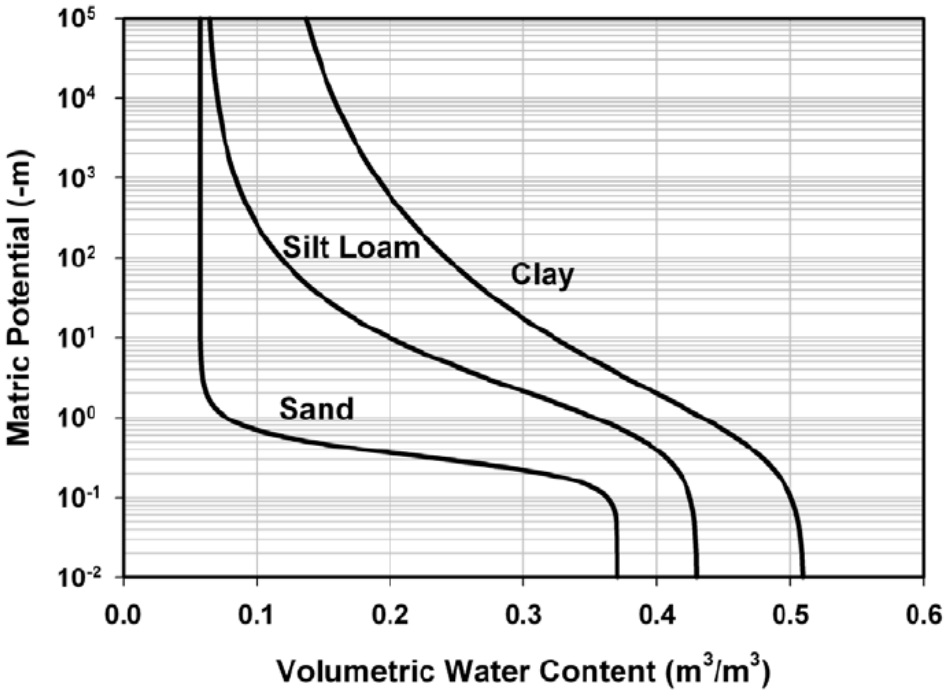

Figure 1.3. Idealized soil-water characteristic curves for soils of different texture (Tuller and Or, 2004)

(b) Effect of drying and rewetting cycles

Drying and rewetting (DRW) of soils occur when dry periods are interrupted by occasional rainfall events. Drying and rewetting cycles are common in arid or semi-arid climates. For example, Mediterranean-type climates as in southern Australia have relatively low rainfall (< 600 mm per annum) and hot dry summers with occasional rainfall events (Butterly et al.,

2011a). Dry soils are characterized by low microbial activity due to low substrate diffusion and water uptake. To counteract the strongly negative soil water potential, some microbes accumulate osmolytes in order to minimise water loss from the cells (Boot, 2011; Warren, 2014). Osmolytes increase the osmotic potential within the cells, hence retaining sufficient water for cell turgor and metabolism (Yan et al., 2015). Upon rewetting, there is a flush of respiration which is due to increased substrate availability from released osmolytes that had been accumulated during the dry period (Yu et al., 2014), cell lysis and exposure of previously occluded soil organic matter after aggregate breakdown (Navarro-García et al., 2012; Yu et al., 2014). Manzoni et al. (2012) suggested that rewetting-induced pulses in nutrient mineralization are important drivers of plant productivity.

The extent of drying and the number of DRW cycles influence the size of the rewetting flush (Yu et al., 2014). Chowdhury (2011) found that rewetting of dry soil induced a respiration flush only if the water potential of the soil before rewetting was about 3-fold lower than water potential for maximum microbial activity. The size of the flush in microbial activity decreases with the number of DRW events (Van Gestel et al., 1993; Butterly et al., 2009). This can be attributed to a number of reasons, such as reduction in microbial biomass, changes in microbial physiology or community composition, or decreasing soil organic matter release (Mikha et al., 2005; Wu and Brookes, 2005; Borken and Matzner, 2009). Changes in microbial community composition may be due to death of some microbes in dry soil or osmotic shock caused by rewetting (Dodd et al., 2015). Shi et al. (2015) concluded that cumulative respiration was strongly influenced by the number or proportion of moist days. When dry and moist periods were of equal length, the difference in cumulative respiration between DRW treatment and constantly moist soil became greater as the total incubation time increased.

Drying and rewetting can influence soil P availability (Chepkwony et al., 2001). Laura (1976) noted that breakdown of soil aggregates upon rewetting could result in increased P availability. Butterly et al. (2011b) reported a short-lived increase in soluble P after rewetting. But there are few and inconclusive reports on the underlying processes. Birch and Friend (1961) suggested that drying and rewetting may stimulate mineralization of soil organic P. In their study, subjecting an organic soil to large series (204) of oven drying-rewetting cycles completely mineralized organic P. Cassman and Munns (1980) noted that P mineralization was greatest when soil water content is near field capacity and declined with soil drying. Olsen and Court (1982) studied the response of resin extractable-P in 16 different soils exposed to 11 DRW cycles, and found lower cumulative resin extractable-P in constantly moist soils than DRW treatments. The higher P availability with DRW may be attributed to an increased solubility of soil organic matter and soil P (Bartlett and James, 1980). Butterly (2008) discussed that P is

released as organic P during the rewetting-induced flush which is mineralised by soil microorganisms to Pi, and can then be taken up by soil microbes or plants, or may be further subjected to physicochemical reactions (e.g. sorption to clay minerals). Kieft (1987) suggested that death of microorganisms could increase soluble P concentration in the soil. In agreement with this, Turner et al. (2003) found that a large proportion of water-extractable organic P was released from lysed bacterial cells after rewetting. Chen et al. (2016) reported that one to three DRW caused a decrease in microbial biomass P (MBP) by 9-41% compared to the constantly moist control. They noted that the treatments with one DRW had larger MBP fluctuation (the highest MBP was 4.2 fold higher than the lowest MBP) than treatments with two and three DRW (where the highest MBP was less than 1.5 fold higher than the lowest), but MBP was lowest after three DRW cycles. The larger fluctuation of MBP with one DRW indicates recovery of MBP after rewetting. Multiple DRW events may have a long-term effect on microbial biomass P because of changes in the microbial community composition (Schimel et al., 2007).

1.5 Organic soil amendments

Decomposition of organic soil amendments is a mainly biologically driven process (Duong, 2009). As described by Kumar and Goh (1999), decomposition of organic amendments releases end products into the biological circulation in the ecosystem. Organic amendment decomposition follows a sequential pattern where the less complex components are decomposed first, followed by the more complex ones. When organic amendments are applied to the soil, soluble organic substances such as sugars, phenolics, hydrocarbons, nutrients and glycerides contained in the amendments are released into the soil solution (Timmons et al., 1970; Couteaux et al., 1995; Schoenau and Campbell, 1996). As the amendment is broken into smaller particles, due to biological activities or external factors (such as cultivation, wind or rain), the surface area is continually increased allowing for rapid microbial colonization. This further leads to mineralization of sugars, low molecular mass phenolic compounds, organic N and P (Shi, 2013).

1.5.1 Effect of residue decomposition on soil properties

Application of crop residue and crop residue management have both a direct and an indirect effect on soil properties.

(a) Improvement of soil physical properties

Soil aggregation and soil structure: Soil aggregation and soil structure are important aspects of soil fertility (Aminiyan et al., 2015). Organic compounds bind with inorganic soil particles

to form microaggregates (<0.25 mm) which then form macroaggregates (>0.25 mm) (Tisdall and Oades, 1982). Carbohydrates, among the various components of soil organic matter, have been shown to significantly increase aggregate stability (Six et al., 2000; Helfrich et al., 2008; Verchot et al., 2011). Puget et al. (1998) found that carbohydrate content was positively correlated with aggregate size, clay, and silt fractions within stable aggregates. Singh et al. (1994) reported greater amounts of large water-stable aggregates, and greater MWD with the application of straw.

Soil compaction and bulk density: Soil compaction is estimated to be responsible for the degradation of about 30% (about 4 million ha) of the wheat belt in Western Australia (Carder and Grasby, 1986; Hamza and Anderson, 2005). The extent of soil degradation is exacerbated by loss of soil organic matter (Virto et al., 2014). Conservation tillage, where crop residues are retained on the soil surface (Conservation Tillage Information Centre CTIC, 2004) or residue incorporation (Sidhu and Sur, 1993; Kumar and Goh, 1999) can reduce soil compaction and soil bulk density. Shaver et al. (2002) showed that soil bulk density decreased with application of crop residues, thus increasing soil porosity and water infiltration (van Donk et al., 2008).

Soil temperature: crop residue management can influence soil temperature (Kumar and Goh, 1999). Surface-applied residues intercept solar radiation and reduce overall soil temperature (Teasdale and Mohler, 1993). However, this effect may become smaller as the residue decomposes (McCalla and Duley, 1946). The increase of the internal mulch temperature could be a significant factor in preventing weed establishment. McCalla and Duley (1946) noted that surface crop residue application during winter could mitigate the effect of extreme sudden changes in air temperature from warm to cold or cold to warm and delay soil freezing and thawing.

Soil water content: Application of crop residues on the soil surface conserves soil water because they reduce water evaporation since less solar energy reaches the soil surface. Crop residue application on the soil surface also reduces the energy of water droplet impacts, thus reducing the detachment of fine soil particles that can result in crust formation (Van Donk et al., 2012). Other benefits of crop residue application on soil water content include increased surface storage of rain or irrigation water, reduction of velocity of runoff water across the soil surface, thus increasing infiltration rate (Steiner, 1994). van Donk et al. (2008) recorded a 1.6 $Mg \cdot ha^{-1}$ increase in maize yield as a result of increased water content under residue-covered soil compared to bare soil. Klocke et al. (2006) reported 63-76 mm water was saved over the growing season due to wheat straw application. However, in a saturated soil, crop residue

addition could limit soil drying and inhibit emergence of plant species sensitive to saturated conditions.

(b) Improvement of soil chemical properties

Soil pH: One of the most important factors determining soil fertility is pH (Kumar and Goh, 1999). Soil pH has been shown to increase with crop residue addition (Bessho and Bell, 1992; Butterly et al., 2013). This has been attributed to the following reasons: (1) Cations that are released during decomposition of organic amendments displace protons and aluminium from exchange sites thus increasing soil base saturation (Bessho and Bell, 1992). (2) Biological decarboxylation of organic acid anions in plant biomass (Yan et al., 1996) consumes protons (Mengel, 1994) (Barekzai and Mengel, 1993). Under aerobic soil conditions, decarboxylation is a major process in organic matter decomposition (Yan et al., 1996). (3) Ammonification of organic N (to produce ammonium) and nitrate uptake increase pH (Hoyt and Hargrove, 1986; Helyar and Porter, 1989). (4) Ligand exchange between hydroxyl groups of aluminium or iron hydroxide and organic anions such as malate, citrate and tartrate (Yan et al., 1996; Tang and Yu, 1999).

Soil organic matter and nutrient availability: Crop residue management is a key consideration when attempting to optimize soil fertility (Schoenau and Campbell, 1996). Crop residues are multi-nutrient sources containing almost all the elements needed by plants, such as N, P, K, S and other micro- and macro-nutrients (Balasubramanian and Nnadi, 1980; Schoenau and Campbell, 1996). Alberto et al. (1996) showed that addition of straw residue improved organic C, total N, available P and exchangeable K compared to bare soil. Kushwaha et al. (2000) found a 28% increase in soil organic C and 33% increase in total N with retention of crop residues compared to removal, after one year. However compared to inorganic fertilizers, nutrient concentrations in crop residues are low.

(c) Improvement of soil biological properties

Microbial processes: Retaining crop residues on the soil surface or incorporation into the soil can stimulate soil microorganisms (Yang et al., 2013); as residue decomposes, the microbial biomass changes (Guo et al., 2016). Such changes have been attributed to the amount and type of crop residue added to the soil. For example, Singh et al. (2015) reported higher soil respiration, organic C, and organic C/microbial biomass C ratio with crop residue than with farmyard manure and vermicompost in a rice-mung bean-wheat cropping system in India. Likewise, Saffigna et al. (1989) found a significant increase in microbial biomass with the application of sorghum residues than in bare soil where residues were removed yearly for 5 years, in central Queensland, Australia. Doran (1980) showed increased microbial density in

about 15 cm depth of an eastern Nebraska soil with the application of maize stover, compared to bare soil and this increase was positively related to the amendment rate.

Activity of soil enzymes have been used as index of soil fertility (Benıtez et al., 2000) since they are involved in the cycling of most important nutrients, and also respond more quickly to changes in soil management than other soil variables (Singh et al., 2015). Hai-Ming et al. (2014) found that soil enzyme activities were affected by residue management practices during early and late rice growth stages in southern China. They showed a significant increase in activities of β-glucosidase, alkaline phosphatase and arylsulfatase with crop residues compared to the unamended control.

1.5.2 Factors influencing residue decomposition rate and nutrient release

Decomposition of plant residues is controlled by three main factors: crop residue composition (chemical properties such as C/nutrient ratios), soil properties (chemical and physical) and climate (temperature, oxygen level and water) (Brussaard, 1994).

(a) Plant residue properties

The decomposition rate of crop residues incorporated into the soil depends on their chemical composition (Kriaučiūnienė et al., 2012). However, Kumar and Goh (1999) found that decomposition rate of plant residues could not be predicted from a single property of the organic material, and that the relative rates of crop residue decomposition were related to combination of these properties.

The most important indicators in crop residue decomposition are the C:N ratio and lignin concentration (Kriaučiūnienė et al., 2012). According to Baldock (2007), crop residues with C:N ratio >40 (or low N) will decompose more slowly than residues with C:N ratio <40 (or high N) (Magid et al., 1997; Yadvinder-Singh et al., 2005). Hence, legume residues that usually have high N content decompose more quickly than cereal residues that have low N content (Yadvinder-Singh et al., 2005).

P mineralization or immobilization after residue addition to soil are dependent on the C:P ratio. High-P residues (>5 mg P/kg, C:P <200) will decompose faster and induce net P mineralisation whereas low-P residues (<5 mg P/kg, C:P >200) can cause net P immobilisation (Tian et al., 1992; Brady and Weil, 2002; Mat-Hassan, 2012). Alamgir et al. (2012) reported increased P immobilization (high microbial P) but decreased P mineralization (low resin P and $NaHCO_3$-Pi) when low-P residue was added to a loamy soil, whereas P mineralization increased with the addition of high-P residues. However, a balance of mineralization and immobilization was attained when medium P residue was added to the soil. This may be due to the residue C/P ratio

(100) which was close to the threshold of P immobilization. Mixing soil with a low C/nutrient residue increased labile P pools two to six-fold compared to amendment with a high C/nutrient residue (Nziguheba et al., 2000; Alamgir and Marschner, 2013a).

The effect of the addition of a given residue may also depend on the properties of the previously added residue. For example, in soil mixed twice with crop residues, when a low C/nutrient residue was followed by a high C/nutrient residue, N and P availability were lower than when a low C/nutrient residue was added to previously unamended soil (Marschner et al., 2015). When low C/P residue followed high C/P residue, nutrients mineralised from the low C/P residue will be rapidly immobilised by microbes decomposing the previously added high C/P residue, reducing nutrient availability, compared to low C/P residue added alone. In contrast, when high C/P residue followed low C/P residue, nutrients mineralized by decomposition of the previously added low C/P residue together with the freshly added high C/P residue lead to higher nutrient availability than with high C/P residue alone. This so-called *legacy effect* is defined as the influence of a previous residues C/nutrient ratio on microbial activity, biomass and nutrient availability after the addition of a second residue with similar or different C/nutrient ratio (Marschner et al., 2015).

Other crop residue qualities such as the lignin (L) and soluble polyphenol (PP) contents have also been shown to influence the rate of residue decomposition and nutrient mineralisation (Constantinides and Fownes, 1994; Clement et al., 1995; Palm et al., 2001; Lynch et al., 2016). According to Tian et al. (1992), high lignin concentration of crop residues reduced decomposition rate and nutrient release (Kumar and Goh, 1999). Saini et al. (1984) also reported lower decomposition rates in stubbles of rice, wheat, and rape than those of their straws due to higher lignin contents. Polyphenols reduce the rate of residue decomposition by binding to proteins and N-containing compounds thus forming complexes resistant to decomposition (Vallis and Jones, 1973; Scalbert, 1991; Yadvinder-Singh et al., 2005). Therefore, C:N, L:N, PP:N and (L+PP):N ratios are negatively correlated with N release from plant residues (Cobo et al., 2002; Nascimento et al., 2011).

(b) Soil and environmental properties

Soil pH: pH is an important factor which influences microbial diversity and community composition (Fierer and Jackson, 2006), therefore affecting the capacity of soil microorganisms to decompose residues (Paul and Clark, 1989; Kumar and Goh, 1999). Soil acidification (pH below 4.5) has a detrimental effect on soil microbes by altering environmental factors such as nutrient availability, element toxicity, organic C characteristics, and vegetation types (Chen and He, 2004; Rousk et al., 2009). Between pH 4 and 7, Rousk et al. (2010) found a positive

relationship between bacterial diversity and soil pH. Parr and Papendick (1978) reported the optimum pH range for rapid decomposition of various organic amendments and crop residues to be between 6.5 and 8.5.

Soil texture: Soil texture indirectly affects the decomposition of crop residues by altering soil water availability, pore size distribution, nutrient availability and surface area (Scott et al., 1996; Yadvinder-Singh et al., 2005). Decomposition of organic residues will be faster in soils with low clay content than clayey soils (Jenkinson, 1977; Yadvinder-Singh et al., 2005). This is because clay protects organic residues from decomposition. Clay reduces the decomposition of crop residues by (i) adsorption on to the inner and outer surfaces of clay particles, and (ii) entrapment of organic substrates between the clay layers (Baldock and Skjemstad, 2000; Lavelle and Spain, 2005), and (iii) formation of aggregates around organic matter particles which prevent biological attack by soil microorganisms (Van Veen and Kuikman, 1990; Mtambanengwe et al., 2004) and thus slows down the decomposition rate and stabilizes soil organic matter.

Temperature: Temperature and soil water content strongly influence mineralization through their effect on microbial activity (Parr and Papendick, 1978; Yadvinder-Singh et al., 2005). According to Paul (2001), activity of decomposers generally increases rapidly from 0 °C to about 30 to 35°C. Roy et al. (2011) reported that increasing temperature from 20°C to 35°C at constant soil water content (field capacity) increased inorganic N content in residue-amended soil. Fierer and Jackson (2006) found temperature sensitivity of residue decomposition was dependent on substrate quality. They found that decomposition of residues with lower quality (or greater lignin content) was more temperature sensitive than that of residues with lower lignin content (Stewart et al., 2015).

Aeration: Good aeration is necessary for activity of aerobic microorganisms involved in the decomposition of organic matter. Soil texture impacts soil aeration, soil structure, and air and water movement, consequently affects the rate of crop residue decomposition (Greenland, 1995). and Waksman (1929) found that corn stalks and rye straw decomposed rapidly under aerobic conditions, but the rate of decomposition was low under anaerobic conditions. (Villegas-Pangga et al., 2000) also found that under flooded conditions, depletion of O_2 decreased the decomposition rate of rice straw. This is because the energy gain from aerobic decomposition is greater than that of anaerobic decomposition.

Soil nutrient availability: The addition of glucose to soil has been used to study the role of C availability in residue decomposition (Jansson, 1960; Macura et al., 1962; Macura et al., 1965). Macura et al. (1965) observed increased C mineralization in treatments where N and P were

added together with glucose, compared to glucose alone. Generally, application of residues with high C:N ratios (low N content) require exogenous supply of N to facilitate decomposition (Yadvinder-Singh et al., 2005). Apart from C and N, new microbial cells also require other inorganic nutrients for growth and development, such as P, K, S, Ca, Mg and other micronutrients (Kumar and Goh, 1999), but the amounts required are much lower than for C and N.

1.5.3 Effect of water content on residue decomposition rate and nutrient release

Changes in soil water content have profound effect on microbial activity (Griffin, 1981). Even at optimum temperature, residue decomposition will be slow if water availability is low (Smith and Elliott, 1990). The optimum water potential for residue decomposition is between −30 and −100 kPa (Yadvinder-Singh et al., 2005). As the soil dries below this water potential range, microbial activity begins to decrease, and it decreases rapidly at water potential below -500 kPa (Wilson and Griffin, 1975; Paul and Clark, 1989; Smith and Elliott, 1990). Quemada and Cabrera (1997) showed that net N mineralization from clover residue increased as water potential increased from −0.03 MPa to −500 kPa. Hood (2001) studied the effects of soil water content on N mineralisation using ^{15}N-labelled soybean residues, and reported a linear increase in percentage N derived from residue as water potential decreased from −800 KPa to −100 KPa. Wheat residue decomposition was also reported to decrease by 35% at −150 kPa and by 90% at −5000 kPa (Stott et al., 1986).

1.6 Detritusphere

1.6.1 Definition

The detritusphere is one of the three hotspots of microbial activity in soil, the other two being the rhizosphere and biopores (Kuzyakov and Blagodatskaya, 2015). Detritusphere and rhizosphere hotspots are due to labile C released by living roots and decomposing organic matter (Kuzyakov and Blagodatskaya, 2015). The detritusphere is defined as a thin layer of soil directly adjacent to plant litter (≤ 5 mm) and is influenced by residue decomposition (Liu et al., 2011) (Fig. 1.4). In the field, the detritusphere could occur for example, under a litter or crop residue layer on the soil surface or around patches of residues incorporated in the soil. Also, root death can transform the rhizosphere into detritusphere (Kuzyakov and Blagodatskaya, 2015). According to Spohn and Kuzyakov (2014), the lifetime of detritusphere hotspots around dead roots is 10-30 days. Gaillard et al. (2003) suggested that the soil matrix provides water,

mineral nutrients such as N and microbial decomposers that colonise the residues, whereas a fraction of the C of the residues is transferred to the soil where it is eventually mineralised.

1.6.2 Nutrient dynamics in the detritusphere

Decomposition can liberate nutrients from plant residues, thus increasing nutrient availability in the detritusphere (Setala and Huhta, 1991; Moore et al., 2003; Wardle et al., 2004). For example, Ball et al. (2014) reported that during decomposition, N concentration in the litter layer correlated with the underlying soil N availability. Petersen et al. (1993) recorded diffusion of soluble organic C from a layer of manure into adjacent soil over time. Similarly, Gaillard et al. (1999) found increased accumulation of ^{13}C and ^{15}N derived from decomposing straw in the adjacent soil, suggesting that molecules released from decomposing residues are transported into adjacent soil mainly through fungal hyphae or diffusion.

de Neergaard and Magid (2015) also reported an increase in water-extractable soil P up to 3 mm from the residue layer as P release from *Rumex* residue increased, suggesting that the increase in water-extractable P is due to P released from the decomposing residue (Haynes and Mokolobate, 2001). Ha et al. (2007) also noted higher available P in detritusphere of high P residue than the bulk soil. However, not all P lost from a decomposing residue remains available. A proportion of P released may be sorbed to soil particles or immobilized by microorganisms.

Mineralization of nutrients immobilized into the microbial biomass could be a potential source of plant available nutrients (Bowman and Cole, 1978). In the detritusphere, compared to the bulk soil, microbial biomass is expected to be several fold higher than in the bulk soil due to the transport of soluble litter C (Poll et al., 2008).

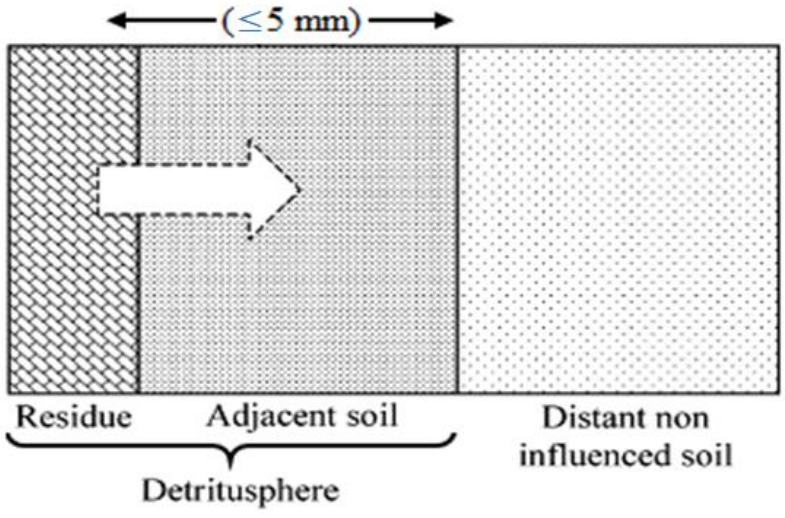

Figure 1.4. Conceptual scheme of nutrient fluxes in the soil. Arrow represents the transfer of nutrients from decomposing crop residues to adjacent soil (Modified from Gaillard et al., 2003).

For example, McMahon et al. (2005) detected greater ^{13}C in the pospholipid fatty acids (PLFAs) of the detritusphere than bulk soil, and it was higher in detritusphere of unleached than leached ryegrass, due to loss of C in the leached residue. Gaillard et al. (1999) showed with low temperature scanning electron microscopy that the microbial biomass was largest near the straw, presumably because of diffusion of soluble compounds from the straw. Ha et al. (2007) also noted higher microbial P in the detritusphere compared to the control soil after application of two legume residues with contrasting P concentrations.

Microbial and enzyme functioning depends on substrate quality (i.e. C/N ratio), which strongly differ in bare soil compared to hotspots such as the detritusphere (Schnecker et al., 2014; Loeppmann et al., 2016; Wang et al., 2016a). Decomposition of crop residues is due to enzymes such as invertase, xylanases, cellulases, pectinases and ligninases (Sinsabaugh et al., 1991; Moorhead et al., 1996). For example, Kandeler et al. (1999) showed that protease, xylanase and invertase activities were two-fold higher in soil under a maize straw layer than in unamended soil. Loeppmann et al. (2016) also found that the catalytic properties of cellulolytic enzymes (β-cellobiohydrolase, β-glucosidase, acid phosphate and β-xylosidase) differed between detritusphere of maize shoot litter and bare soil.

1.7 Influence of plant growth on nutrient availability in the detritusphere: The rhizosphere/detritusphere interface

Effect of plants on nutrient availability in the rhizosphere

The rhizosphere is the region within approximately 2 mm distance from the root surface (Hiltner, 1904; Dotaniya and Meena, 2015). It is one of the three hotspots of microbial activity in the soil (Kuzyakov and Blagodatskaya, 2015) due to the presence of high concentrations of easily available compounds released from the roots compared to the bulk soil. These easily available compounds include carbohydrates (sugars and oligo-saccharides), amino acids, organic acids, vitamins, nucleotides, flavonoids, enzymes, hormones and volatile compounds (Prescott, 1999; Osorio Vega, 2007). These compounds are a source of food and energy for soil microorganisms (Rillig et al., 2007; Chowdhury et al., 2009; Shukla et al., 2013) and aid the mobilization of plant available nutrients (Paterson et al., 1997; Piirainen et al., 2007).

In the rhizosphere, there are different groups of plant beneficial microorganisms. For example, those that are able to solubilize insoluble P forms, thus playing important role in P availability (Dotaniya and Meena, 2015). The rhizobium bacteria convert atmospheric dinitrogen into

ammonia, which is transferred to their symbiotic plant partners (Hirsch et al., 2001; Jones et al., 2007; Oldroyd and Downie, 2008). The mycorrhizal fungi assist plants in obtaining water, P and other micronutrients from the soil and in return receive organic C from the plant (Harrison, 2005; Rillig and Mummey, 2006; Maillet et al., 2011).

Low molecular weight organic compounds in the rhizosphere can mobilize nutrients. For example, organic acid anions released by plant roots or during decomposition of dead roots compete with P sorbed onto metal oxides (Bolan et al., 1994; Hinsinger, 2001), resulting in release of P into soil solution for plant (and microbial) uptake. Further, organic acids have been implicated in the detoxification of metals by plants (e.g., Al), microbial proliferation in the rhizosphere, and the dissolution of soil minerals in pedogenesis (Marschner, 1995; Jones, 1998). Amino acids found in the rhizosphere as a result of lysis or cellular efflux from plants and microbes or proteolysis of existing peptides are mainly used as N source than as C source by microorganisms (Hamer and Marschner, 2005; Moe, 2013). Amino acids are deaminated by extracellular enzymes (e.g., amino acid oxidase), releasing NH_4-N, which is readily taken up by plants and microbes or further oxidized to nitrate (Jones and Kielland, 2012; Moe, 2013).

Nutrients released by exudates or microbes are taken up by plant roots or immobilized into the microbial biomass, leading to the formation of a depletion zone around the roots. This depletion zone gradually widens and may interact with that of neighbouring roots (Darrah, 1993). Nutrients are usually present in relatively large amounts in the bulk soil compared to the rhizosphere (Rengel, 2001). As nutrients are depleted in the rhizosphere, they are being replenished by diffusion of nutrients from the bulk soil; the diffusion rate increases with the concentration gradient, transporting larger amounts of nutrients towards the roots (Rengel and Marschner, 2005). Barber et al. (1963) suggest that the amounts of nutrients that are moved to the plant root depend upon the amount of water used by the plant and the concentration of nutrients in the water.

Effect of plants on nutrient availability in residue amended soil.

Addition of crop residues has been shown to influence microbial activities and nutrient availability in the rhizosphere. The mechanisms by which crop residues and soil organic matter (SOM) decomposition influence the rhizosphere have been reviewed in detail by Dormaar (1990) and Cheng and Kuzyakov (2005). Cheng and Kuzyakov (2005) showed that SOM decomposition in the rhizosphere could be decreased by 10-30% or increased by as much as 100% compared to that in non-rhizosphere soil. Residue decomposition is hypothesised to be higher in the rhizosphere due to higher microbial activity (Farrar et al., 2003) induced by inputs

of labile compounds exuded from the roots. This has been termed rhizosphere priming effect (Kuzyakov et al., 2000). For example, in a rhizosphere model, Kuzyakov et al. (2007) found that the addition of malate and glutamate, compounds found in root exudates, increased the mineralization of *Lolium perenne* shoot residues by about 20% compared to the soil without these compounds. Hamer and Marschner (2005) showed that addition of organic substrates representative of root exudates (fructose, alanine, oxalic acid and catechol) enhanced the mineralization of SOM in both surface and subsoil horizons by about 10-63%. Studies have linked higher microbial functional diversity as well as higher activity of microbial enzymes to faster rates of residue decomposition (Dodor and Tabatabai, 2003; Acosta-Martinez et al., 2014; McDaniel et al., 2014). Such effects are driven mainly by higher labile C availability which support a larger and more active microbial biomass in the rhizosphere (Hoyle et al., 2008), thus increasing residue decomposition, compared to soil with only residue addition.

Microbial decomposition of crop residues can provide an important source of nutrients for plants and other organisms (Noack et al., 2012). However, the fate of nutrients in the rhizosphere depends on the quality (C/nutrient ratio) of the added crop residues. Crop residues with C/N > 25 and C/P > 200 are decomposed slowly and induce temporary net nutrient immobilization in the microbial biomass (Trinsoutrot et al., 2000; Alamgir et al., 2012; Chen et al., 2014). For example, Marschner et al. (2012) reported depletion of inorganic N in the vicinity of wheat residue (C/N 74) and maize roots, which was explained by immobilization of N in the microbial biomass and uptake by roots. In the study by Alamgir and Marschner (2013b), amendment of soil with faba bean (C/N 12) residue increased plant growth and nutrient uptake as well as microbial nutrient uptake compared to unamended soil. Soil amendment with white lupin residue (C/N 40) on the other hand increased microbial nutrient uptake, but resulted in low plant N uptake. Addition of mature faba bean (C/P 211) or mature chickpea (C/P 618) residues induced P immobilization and reduced available P and plant P uptake (Hasbullah et al., 2011).

1.8 Aims of this study

The incorporation of plant residues into the soil after harvesting can improve soil properties, and also return nutrients to the soil, especially P, which is often limiting plant growth in agricultural soils. More information is needed especially on P pools that can be mobilised by plant and microbial exudates and therefore important for long-term P availability. A more comprehensive understanding of P release from residues into soil is needed, especially into the detritusphere. The effect of chemical composition and soil water availability on nutrient release

from organic materials mixed into the soil has been studied. However, the effect of water availability on P pools in the detritusphere is still unclear. Surface applied residues may be removed by erosion or animals and replaced by other residues. Little is known about the effect of a change in residues on P pools in the detritusphere. Lastly, the influence of plant roots on P pools in the detritusphere of crop residues is not well described.

The overarching aim of this study is to determine the influence of water availability, crop residue quality and plant growth on P pools in the detritusphere of crop residues with different potentials to release P during decomposition (Fig. 1.5).

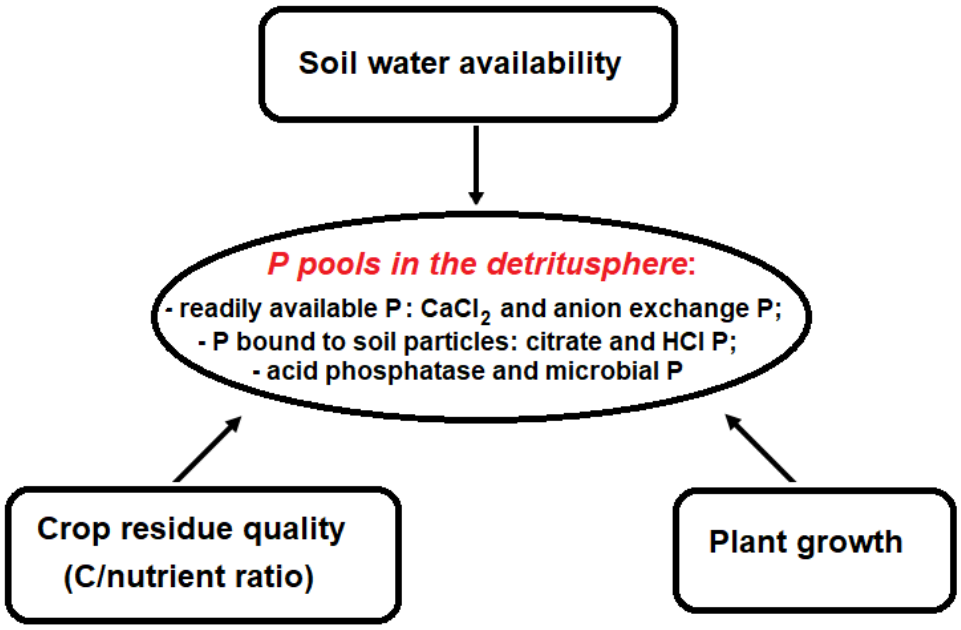

Figure 1.5. Schematic diagram of the factors influencing P pools in detritusphere soils assessed in this study.

In order to achieve the aim mentioned above, the objectives of this research project are to determine the effects of the following factors on P pools and transformations in the detritusphere:

- Drying and rewetting (Chapter 2),
- water availability (Chapter 3),
- Addition of inorganic N and P, alone or in combination (Chapter 4),
- Replacement of one residue with another without soil disturbance (Chapter 5), and
- Presence of wheat roots (Chapter 6).

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Chapter 2. Influence of drying and rewetting on soil P pools in the detritusphere of crop residues.

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

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ORIGINAL PAPER

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

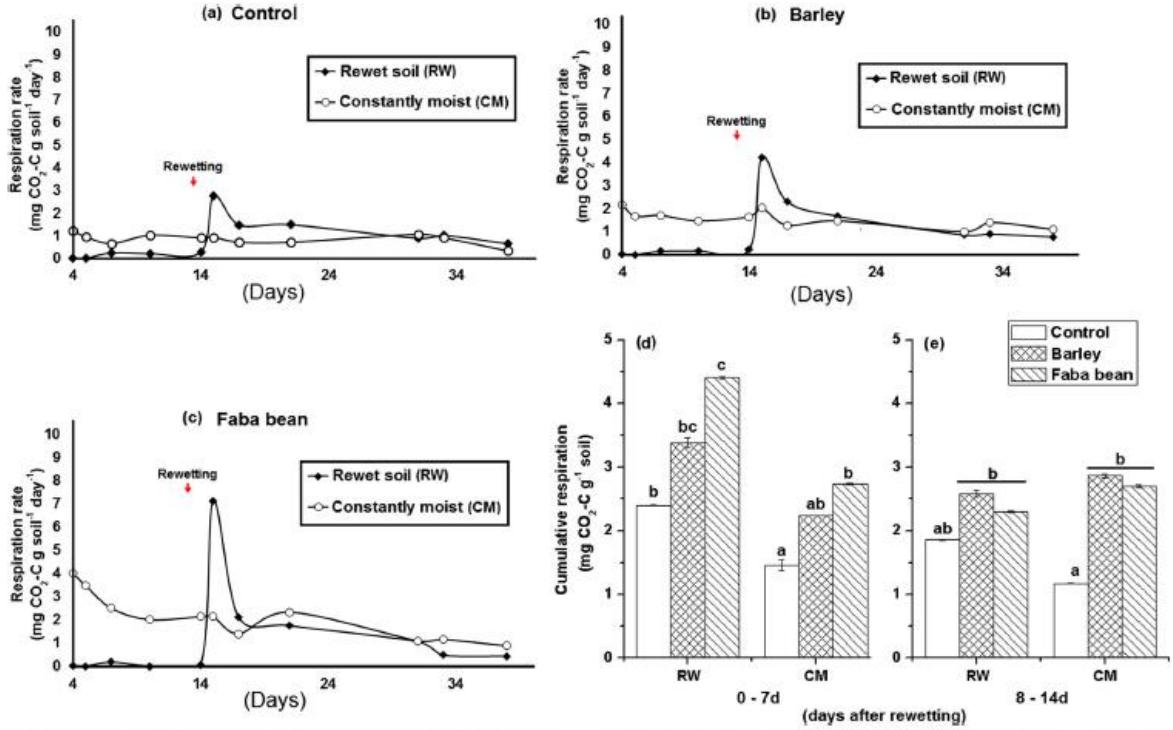

Fig. 1 Respiration rate after rewetting (RW) following a 14-day dry period, or maintained constantly moist (CM) in unamended control (**a**), detritusphere soils of barley (**b**) and faba bean residue (**c**) cumulative respiration (**d**) from day 0 to day 7 and day 8 to 14 after rewetting in control, 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 fourfold 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.

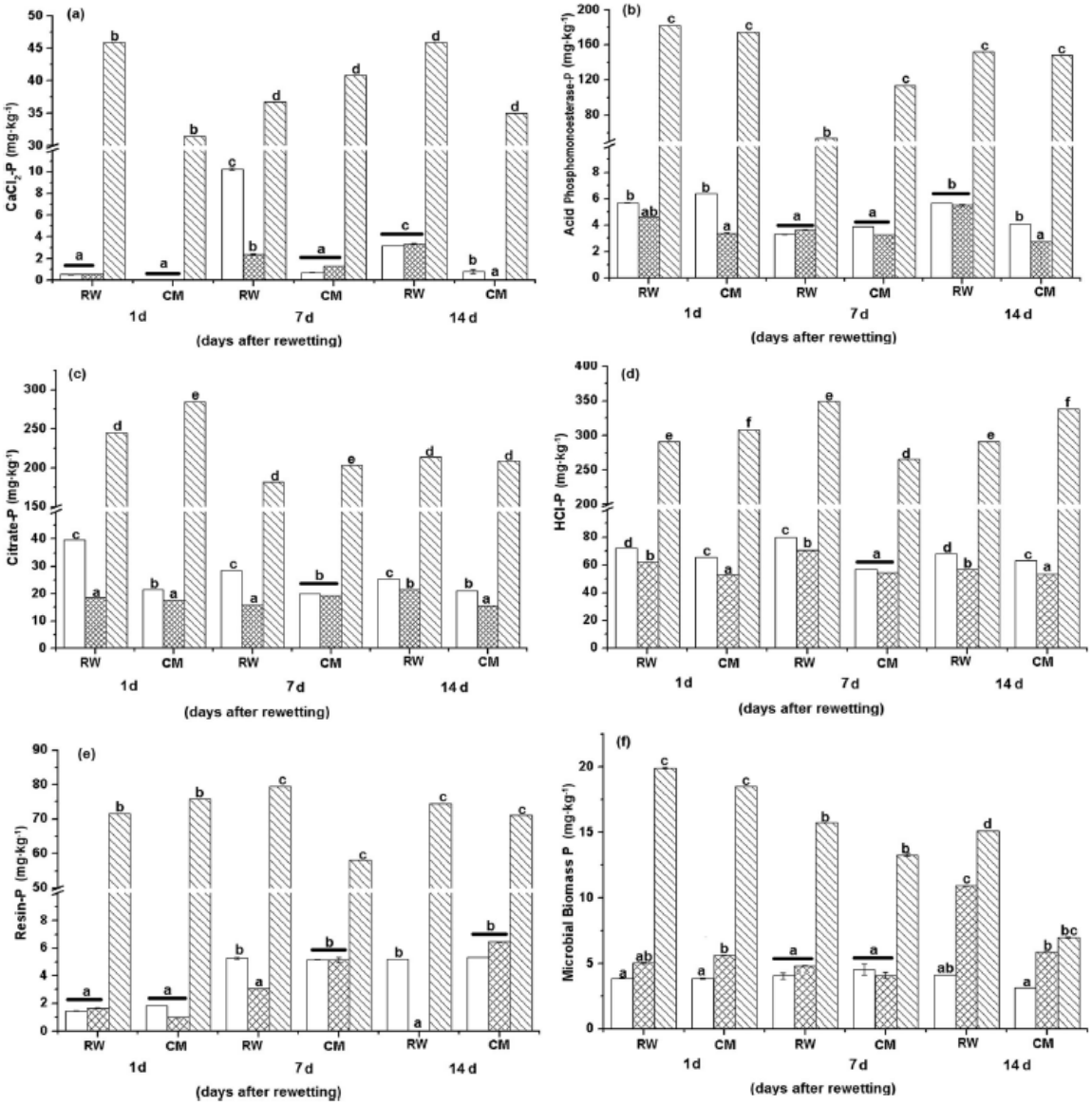

Fig. 2 $CaCl_2$-P (a), acid phosphomonoesterase-P (**b**), citrate-P (**c**), HCl-P (**d**), resin-P (**e**) and microbial biomass P (**f**) in control, barley and faba bean detritusphere soils, 1, 7 and 14 days after rewetting (RW), or in constantly moist (CM) soils. For each sampling time separately,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

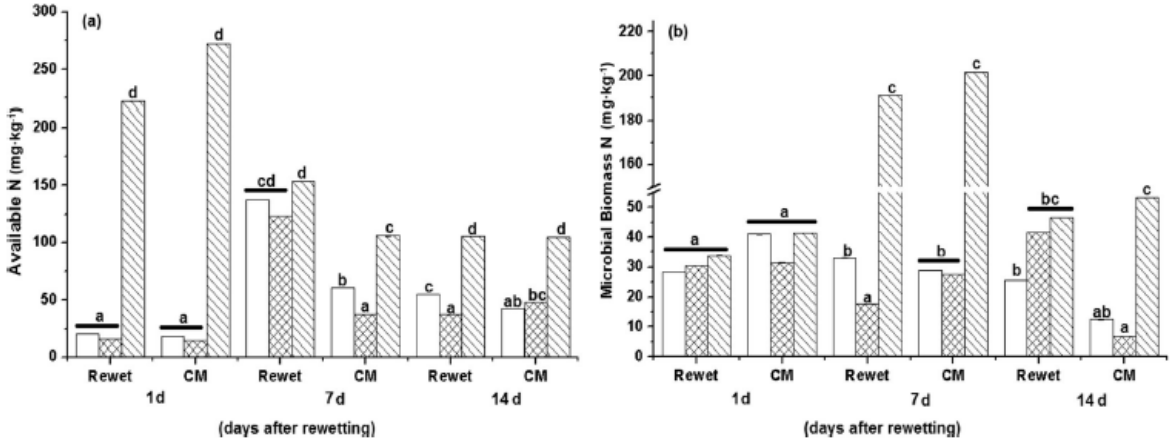

Fig. 3 Available N (**a**) and microbial biomass N (**b**) in control, barley and faba bean detritusphere soils, 1, 7 and 14 days after rewetting (RW), or in constantly moist (CM) soils. For each sampling time separately, columns with different letters are significantly different ($P \geq 0.05$, $n =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

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

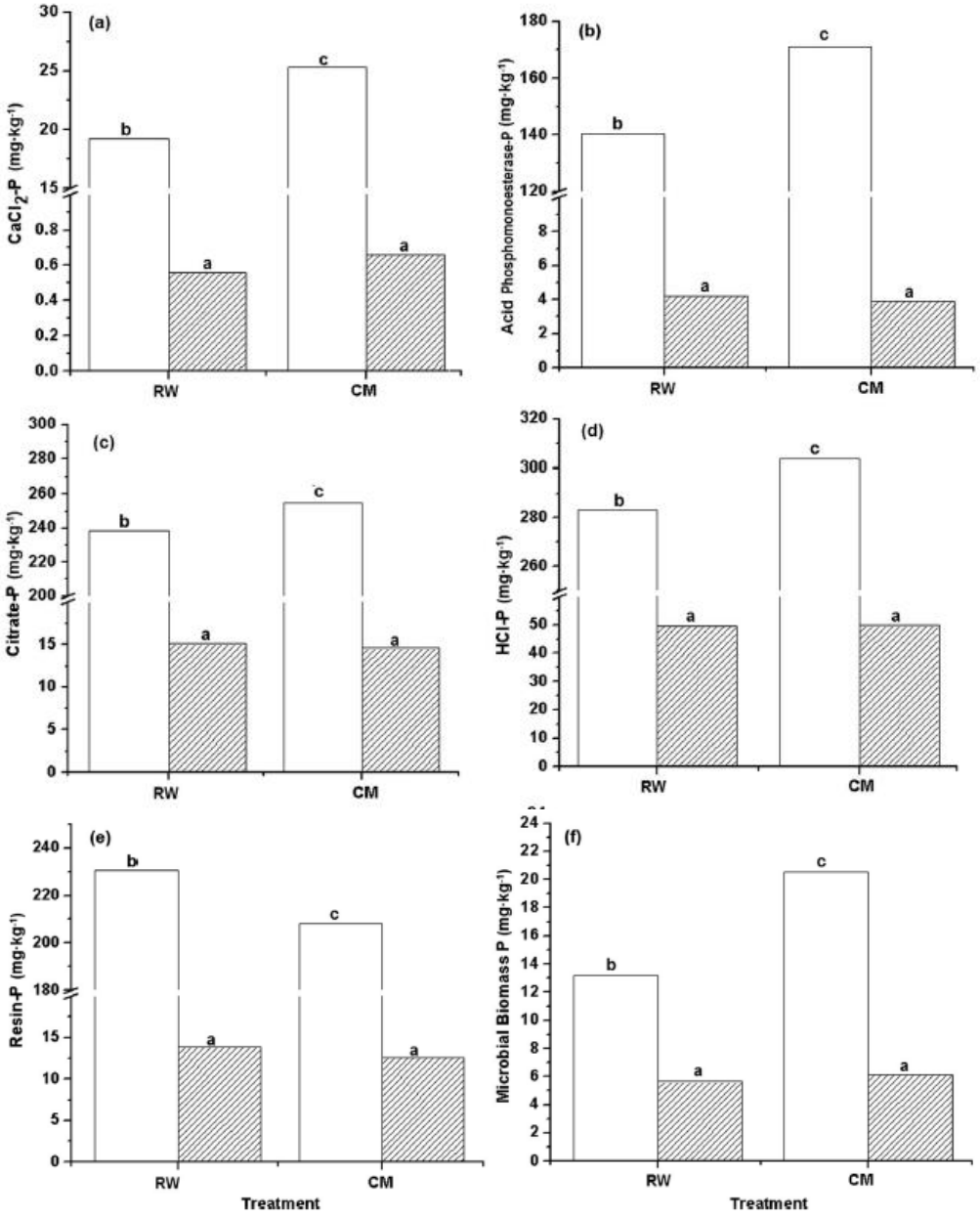

Fig. 4 $CaCl_2$-P (**a**), acid phosphomonoesterase-P (**b**), citrate-P (**c**), HCl-P (**d**), resin-P (**e**) and microbial biomass (**f**) P in control soil ☐ and faba bean ▨ detritusphere and, 4 days after rewetting (RW), or in constantly moist (CM) soils after placement of resin strips for 4 days. 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 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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Chapter 3. Influence of soil water availability on P pools in the detritusphere of crop residues.

Soil water availability influences P pools in the detritusphere of crop residues with different C/P ratios.

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Overall percentage (%)	**75%**		
Certification	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligation or contractual agreements with a thrid party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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By signing the Statement of Authorship, each author certifies that:

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ii. permission is granted for the candidate to include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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ORIGINAL PAPER

Soil Water Availability Influences P Pools in the Detritusphere of Crop Residues with Different C/P Ratios

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Abstract
Little is known about the effect of water availability on P pools in the detritusphere. Detritusphere was generated with two plant residues: 100% barley straw, C/N 95, C/P 255; 75% barley straw with 25% young faba bean shoot, C/N 74, C/P 200. Residues were placed between two PVC caps filled with soil at − 0.078 MPa, separating them from the soil surface with fine nylon mesh. Unamended controls were without residue between the two meshes. After 2 weeks, soil at 0–2 mm distance from the surface was collected and the soil water availability was either maintained at − 0.078 MPa or reduced to − 0.320 and − 1.700 MPa by drying in a fan-forced oven. Bioavailable P pools, available N, and microbial N were measured 1, 14, and 28 days after adjusting to different water availabilities. Soil respiration was measured over 28 days. Soil water availability had a stronger effect on respiration, available N, and microbial biomass N (MBN) in the mix than the control or barley. With the mix compared with − 1.700 MPa, cumulative respiration from day 0 to 14, available N and MBN were five, two, and three-fold higher at − 0.078 MPa. In the control or with barley, differences between the two water contents were two or less fold. Low water availability limits microbial activity and nutrient fluxes at high substrate availability as in the mix but has little effect when substrate availability is low even at high water availability as in the control and with barley.

Keywords Nutrient availability · Substrate supply · Water availability

1 Introduction

Dry periods are common in Mediterranean ecosystems and their intensity and frequency are expected to increase in the future (Houghton et al. 2001). Soil water content is a major factor affecting soil nutrient availability (Clancy et al. 1995; Díaz and Roldán 2000; Schimel et al. 2007) and decomposition of organic amendments through its effect on microbial activity.

Soil water availability is best described as soil water potential (McLaren and Skujins 1968). At low soil water content, water potential is more negative (lower) because water is bound more tightly to soil particles and held in smaller pores than at high water content (Brady and Weil 2002). Thus, water is less available for microbes as water potential becomes more negative. At low soil water content, substrate diffusion is restricted due to the thin water films around aggregates and water may be drawn out of microbial cells. Consequently, soil water content is an important regulator of microbial activity. But at or above saturation, microbial activity is low due to poor aeration and limited availability of O_2 (Rovira 1953). The effect of water availability on soil nutrient availability and microbial activity has been studied extensively using bulk soil samples. For example, Poll et al. (2008) showed that litter mass loss declined with soil water content. Soil respiration declines with decreasing (more negative) water potential (Christian and Waltho 1966; Mozumder and Caroselli 1970).

In experiments where crop residues were mixed into soil and maintained at water content optimal for microbial activity, residues with C/P above 200 induce net P immobilisation and depletion of available P (Khuyen and Marschner 2017). In contrast, decomposition of residues with lower C/P ratio results in higher P availability and other P pools (Alamgir et al. 2012; Umrit and Friesen 1994). During decomposition of crop residues, P availability increases in the soil due to (i) release of P, (ii) exchange of organic acid anions produced during residue decomposition with sorbed P (Bolan et al. 1994; Hue et al. 1994), and organic acid anions forming metal complexes which reduces P sorption. For example, compared to unamended soil, mixing of soil with low (63; faba bean) or

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medium (232; chickpea) C/P crop residues increased available P, labile P pools, microbial P, and $NaHCO_3$-extractable inorganic P (Alamgir and Marschner 2013). But these P pools were little affected by amendment with high C/P residue (640; white lupin). Decomposition rate of residues is not only influenced by the C/nutrient ratio, but also by their organic C composition as cellulose or lignin is more difficult to decompose than less complex or water-soluble compounds (Xu et al. 2017). Mature plant residues such as straw have a higher concentration of cellulose and lignin than residues of young plant tissues (Rencoret et al. 2011).

The detritusphere is defined as the layer of soil directly adjacent to the decomposing crop residue (< 5 mm into the soil), and usually characterised by a higher concentration of easily available compounds than the bulk soil, particularly in the early stages of residue decomposition (Poll et al. 2010; Liu et al. 2011). For example, C and N turnover can be higher within a distance of 3–4 mm from litter than in bulk soil (Gaillard et al. 1999; Kandeler et al. 1999). However, little is known about the influence of water availability on P pools and P dynamics in the detritusphere of crop residues with different C/P ratios. In the field, the detritusphere is an important interface between soil and crop residues, for example under a layer of residues on the soil surface or around residue clumps in the soil. Particularly in semi-arid regions, water availability in the top soil can vary depending on rainfall and temperature (Sun et al. 2017). When crop residues are used to improve plant nutrient uptake, it is important to understand nutrient availability in the detritusphere at different water availabilities.

We hypothesised that (1) soil respiration, microbial biomass, and P pools are greater at high (− 0.078 MPa) than low (− 1.700 MPa) water availability, due to higher water and substrate availability, and (2) the difference in soil respiration, microbial biomass, and P pools between high (− 0.078 MPa) and low (− 1.700 MPa) water availability will be greater with low C/P residue than one with high C/P ratio. The second hypothesis is based on the assumption that with high C/P residue, substrate availability will limit soil respiration, microbial biomass, and P pools.

2 Materials and Methods

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); the site had been under permanent pasture over 80 years but recently cropped with oats. This area has a Mediterranean climate, characterised by cool, wet winters and hot, dry summers with occasional short, heavy rainfall events. The soil is a Chromosol in Australian soil classification and a Rhodoxeralf in US Soil Taxonomy. Soil from six different sites was combined and mixed. The soil was dried at 40 °C and sieved to 2 mm. The properties of the soil are as follows: pH 6.8 (1:5 soil/water), EC (1:5) 0.1 dS m^{-1}, clay 25%, sand 37%, silt 37%, total P 302 mg kg^{-1}, total organic C 17 g kg^{-1}, total organic N 1.5 g kg^{-1}, bulk density 1.3 g cm^{-3}, and maximum water holding capacity (WHC) 349 g kg^{-1}.

2.1 Experimental Design

Detritusphere soil was generated over 14 days at − 0.078 MPa to maximise the effect of the crop residues on detritusphere soil properties. Two crop residues used are mature barley straw (*Hordeum vulgare* L.) alone or mixed with young faba bean residue (*Vicia faba* L.) at a 75:25 ratio. The mix was used because, in a previous study, faba bean alone had resulted in very high P pools and N availability compared to barley alone (Erinle et al. 2018). Results of the two residues could only be statistically compared after log-transformation of the data. The residues were dried in a fan-forced oven (40 °C) ground and then sieved to 0.25–2 mm (Table 1).

Detritusphere soil was generated in microcosms as described in Ha et al. (2007) and Erinle et al. (2018). Briefly, 90 g dry soil was filled into caps of PVC tubes (2 cm height, 7 cm diameter) and packed to a bulk density of 1.3 g cm^{-1}. To activate the soil microbes, reverse osmosis (RO) water was added to achieve 50% WHC (equivalent to − 0.078 MPa), then the soil was incubated in the dark at 20–25 °C for 7 days during which it was maintained at 50% WHC. In other experiments with this soil, soil respiration was maximal at − 0.078.

After the pre-incubation, the open ends of the PVC caps were covered with fine nylon mesh cut into circles (mesh size 0.1 mm × 0.8 mm; ⌀ = 85 mm). Barley residues alone or the 75:25 mix of barley and faba bean residue (3.6 g per microcosm, equivalent to 20 g kg^{-1}) were spread on the mesh of one PVC cap and then covered by the open end of a second. The

Table 1 Total organic C, N, P, water extractable P, C/N ratio, C/P ratio of high C/P (mature barley straw alone), and low C/P (barley straw mixed with young faba bean residue at a 75:25 ratio) residues ($n = 4$). Different letters indicate significant differences between residues ($P \leq 0.05$) (from Erinle et al. 2018)

Properties	Barley straw	Mix
Total organic C (g kg^{-1})	408b	392a
Total N (g kg^{-1})	4.3a	12.9b
Total P (g kg^{-1})	1.7a	3.6b
Water extractable P (g kg^{-1})	0.1a	1.7b
Water extractable organic C (g kg^{-1})	20a	24a
C/P ratio	255b	110a
C/N ratio	95b	31a
Cumulative respiration (mg CO_2-C g $residue^{-1}$)	344a	785b

open ends of the PVC caps were pressed together and secured with rubber bands. With this residue amount, a thin residue layer covered the entire mesh area and the cap ends could be closely fitted to avoid loss of residue during the experiment Thus, the thin layer of residue was between the two open ends of the caps, separated from the soil by nylon mesh. The control had no crop residue between the meshes. The microcosms were placed in the dark at 20–25 °C for 2 weeks during which soil moisture was maintained at − 0.078 MPa by weight. The closed ends of the PVC caps had four holes to allow gas exchange and addition of water to maintain the soil water content. The two-week duration was used because, in a preliminary study, detritusphere P pools changed little after 2 weeks (data not shown). After 2 weeks, the two PVC caps were separated and the two layers of mesh with the residues in between were removed without disturbing the soil surface. Residue dry weight after 2 weeks was 2.7 g for barley straw and 2.1 g for the mix. Soil in 0–2 mm from the surface was collected as the detritusphere soil. Fifteen grams of soil were collected from each of the two PVC caps of a microcosm which were combined to 30 g per replicate for the following period.

Detritusphere soil (30 g) was placed into PVC cores (1.85 cm radius, 5 cm height) which had one end covered by nylon mesh base (7.5 μm, Australian Filter Specialist); soil bulk density was adjusted to 1.3 g cm^{-1}. Then soil water availability was either maintained at − 0.078 MPa or adjusted to − 0.320 MPa and − 1.700 MPa by placing the cores in a fan-forced oven at 30 °C for 4 and 10 h, respectively. This water availability was maintained in the following 28 day period by weight and adding water if necessary. These water availabilities were selected because Xue et al. (2017) showed that respiration and microbial growth in this soil decreased with decreasing soil water availability from − 0.078 to − 1.700 MPa in planted and unplanted soil. Cores were destructively sampled for analyses 1, 14, and 28 days after adjusting to different water availabilities. There were four replicates per treatment and sampling time. After reaching the desired water content, cores sampled on day 1 were placed individually into 1-L jars with gas-tight lids which had septa to allow quantification of the headspace CO_2 concentration (see below). The jars were incubated in the dark at 20–25 °C. After removal of the cores on day 1, the cores for the day 14 sampling were placed in the jars. This was repeated on day 14, placing the cores for the day 28 sampling in the jars. Cores not in jars were incubated in the same conditions in trays.

2.2 Measurements

Analyses were carried out as described in Erinle et al. (2018). Soil maximum water holding capacity was measured matric potential = − 10 kPa (Wilke 2005). Soil texture was determined according to Ge and Or (2002). Soil pH was determined in a 1:5 (*w*/*v*) soil to reverse osmosis (RO) water ratio (Rayment and Higginson 1992). Total organic C of soil and residues was determined by wet oxidation (Walkley and Black 1934). Total N in soil and plant residues was determined using the Kjeldahl method (McKenzie and Wallace 1954). Total P in soil and plant residues was determined by digesting samples with a mixture of HNO_3 and $HClO_4$ and measured in the digest by the phosphovanadomolybdate method (Hanson 1950). To determine water-soluble P in the residues, 30 mL of hot (85 °C) RO water was added to 1 g residue, then shaken for 2 h and filtered through a Whatman #42 filter paper (modified from Konieczynski and Wesolowski 2007). The filtrate P concentration was measured colorimetrically (630 nm) using the malachite green method (Ohno and Zibilske 1991). Water extractable carbon was determined following a similar procedure, but with 0.25 g residue. Organic C in the filtrate was determined by the Walkey and Black method.

Soil respiration was measured as described in Setia et al. (2011) using a Servomex 1450 infra-red analyser (Servomex Group, Crowborough, UK). Linear regression based on the injection of known amounts of CO_2 in similar jars was used to define the relationship between CO_2 concentration and analyser reading. Residue decomposition was measured separately using 3.6 g residue mixed with 1.8 g soil. Respiration was measured over 2 weeks as described above. Cumulative respiration was about twofold higher with the mix than with barley (Table 1).

Soil P pools were measured using a modification of DeLuca et al. (2015). Two pools of the DeLuca method were not measured. $CaCl_2$ P (representing the soluble and weakly adsorbed inorganic P) was replaced by anion extractable P, both are available P pools. Instead of phosphatase labile organic P, microbial biomass P was measured because we found in earlier studies that the phosphatase P concentration in this soil was very low and variable. Biomass P is a potentially available P pool from which P is released upon biomass turnover. To determine Citric acid- and HCl-extractable P, 0.5 g of soil was extracted in parallel by shaking with 10 ml of each extractant (10-mM citric acid or 1 M HCl, respectively) on an end-over-end shaker in separate 50-mL falcon tubes for 3 h. P pools extracted are potentially bioavailable inorganic P pools sorbed to clay particles or weakly bound in inorganic precipitates, respectively. Two other pools, resin (available) P and microbial biomass P (MBP), were determined using the anion exchange resin method (Kouno et al. 1995) with hexanol fumigation. The P concentration in the extracts was by the malachite-green method as described in Ohno and Zibilske (1991). MBP is the difference in P concentration between fumigated and un-fumigated soil (Kouno et al. 1995). No correction factor was used because the

recovery of a P spike in this soil was 98% (Butterly et al. 2010). Available N (ammonium and nitrate) concentration was measured after 1 h shaking with 2 M KCl in a 1:5 soil to extractant ratio. Ammonium-N and nitrate-N were determined after Willis et al. (1996) and Miranda et al. (2001), respectively. Microbial biomass N was determined by chloroform fumigation-extraction with 0.5 M K_2SO_4 at 1:4 soil to extractant ratio (Moore et al. 2000) followed by ammonium in the extract according to Willis et al. (1996). Microbial biomass N is the difference in NH_4^+ concentration between fumigated and non-fumigated samples divided by 0.57 (Moore et al. 2000).

2.3 Statistical Analysis

There were four replicates per treatment and sampling time. Data was analysed by two-way repeated measures ANOVA with fixed factors water availability (−0.078 MPa, −0.320 MPa, and −1.700 MPa) and residue treatment (control without residue, barley, and barley+faba bean residues). Separately for each sampling time, Tukey's multiple comparison test was used to significant effects among treatments ($P \geq 0.05$). The statistical analyses were carried out in Genstat v18.2 (VSN International Ltd., UK).

3 Results

Compared with the control, respiration rates were about twofold higher with barley and threefold higher with the mix (faba bean:barley residue at 25:75) (Fig. 1a–c). Respiration rates were stable in the control but declined over time with residues, particularly with the mix. At −0.078 MPa compared with −1.700 MPa, respiration rates were about fivefold higher with the mix, threefold with barley and twofold higher with the control. Water availability had no effect on cumulative respiration in the control or with barley (Fig. 2). With the mix, where cumulative respiration was two to threefold higher than in the control, cumulative respiration was about fivefold higher at −0.078 MPa than at −1.700 MPa.

One day after water availability adjustment, P pools, MBP, and available N were higher with the mix than in the control at all water availabilities (Fig. 3). There was little or no difference in P pools, available N and MBN between control and with barley. In all residue treatments (residues and control), citrate-P was about 10% higher at −1.700 MPa than with higher water availability (Fig. 3a). Citrate-P was about threefold higher with the mix than the control or with barley. HCl-P decreased with increasing water availability and was about 20% higher with −1.700 MPa than at −0.078 MPa. HCl-P was about 40% higher with the mix than in the control and with barley (Fig. 3b). In all residue treatments, resin-P was

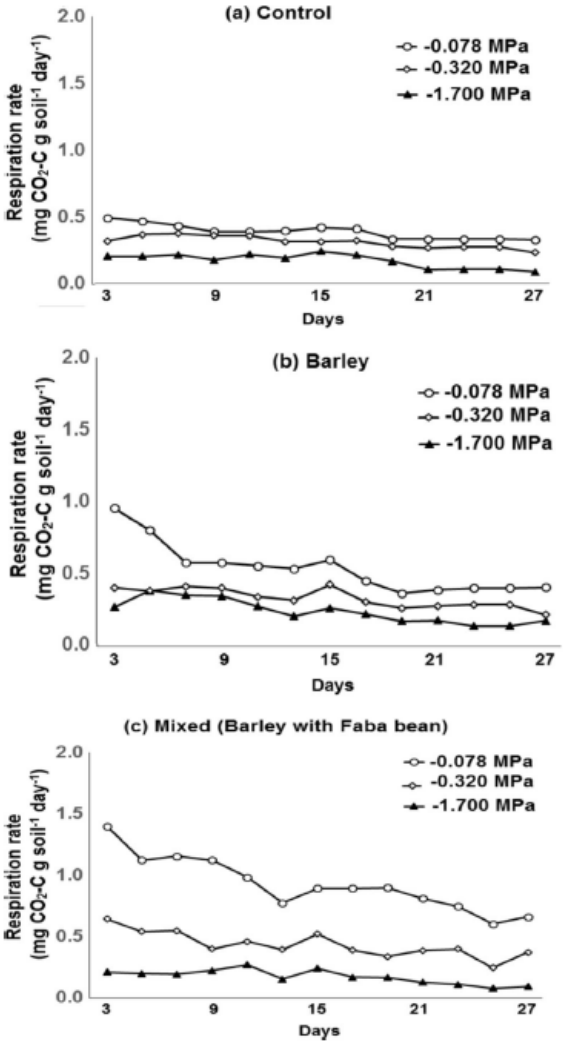

Fig. 1 Respiration rate over 28 days in **a** unamended control, **b** detritusphere soil of mature barley straw, and **c** detritusphere of barley straw + faba bean residue (ratio 0.75:0.25) at different water availabilities (−0.078 MPa, −0.320 MPa, and −1.700 MPa) ($n = 4$)

about twofold higher at −1.700 MPa than at −0.078 MPa. Resin-P was two to threefold higher with the mix than with barley or the control (Fig. 3c). In the control and with the mix, MBP was higher at −0.078 MPa than −1.700 MPa with greater differences in the control than the mix (Fig. 3d). MBP with barley was not influenced by water availability. Compared to the control, MBP with barley was threefold higher at −1.700 MPa and 25% higher at −0.078 MPa. With the mix, MBP was two to threefold higher than the control at −1.700 MPa and −0.078 MPa.

Only in the mix, available N was higher at −1.700 MPa than at −0.078 MPa, where it was about twofold higher at −1.700 MPa (Fig. 3e). Available N 1 day after water

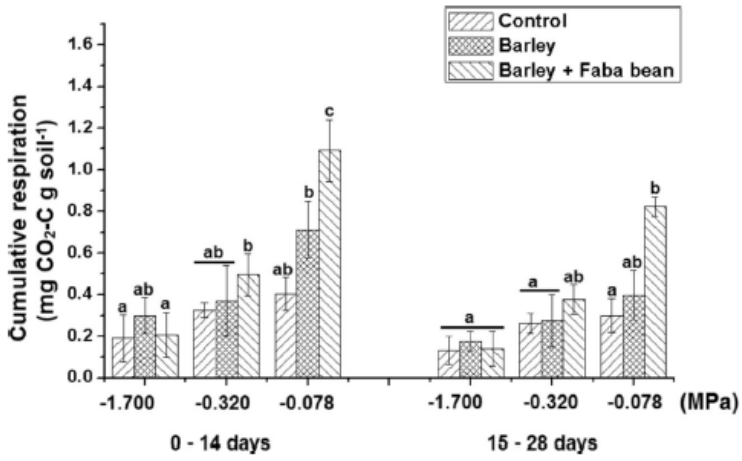

Fig. 2 Cumulative respiration from day 0 to 14 and day 15 to 28 in control and detritusphere soil of barley and barley-faba bean mix at different water availabilities (− 0.078 MPa, − 0.320 MPa, and − 1.700 MPa). Columns in with different letters are significantly different ($P \geq 0.05$, $n = 4$)

availability, adjustment was about 10-fold higher with the mix than in the control or with barley. In all residue treatments, MBN was lowest at − 1.700 MPa. MBN did not differ between control and detritusphere at − 1.700 and − 0.320 MPa, but was about twofold higher with the mix than in the control and with barley at − 0.078 MPa (Fig. 3f).

At all water availabilities, citrate-P, HCl-P, and resin P 14 and 28 days after water availability adjustment were between two and threefold higher with the mix than in the control which differed little from barley detritusphere (Fig. 4). The only exception was citrate-P at − 0.078 MPa on day 14 which was 50% lower with barley and 30% higher with the mix compared to the control (Fig. 4a). On day 14, citrate-P with barley and the mix was about 20% higher at − 1.700 MPa than at − 0.078 MPa. But in the control, it was 40% higher at − 0.078 MPa than at − 1.700 MPa. On day 28, citrate-P was not influenced by water availability. HCl-P on day 14 was 10–20% higher at − 1.700 MPa than at − 0.078 MPa with the mix and barley (Fig. 4b). HCl-P in the control on day 14 and in all residue treatments on day 28 was not influenced by water availability. Resin-P with barley and the mix was about 10–20% higher at − 1.700 MPa than at − 0.078 MPa on days 14 and 28 (Fig. 4c). In the control, resin-P was 20% higher at − 1.700 MPa than at − 0.078 MPa on day 14 but not influenced by water availability on day 28. MBP on day 14 was about 25% lower at − 1.700 MPa than at − 0.078 MPa in all residue treatments (Fig. 4d). But on day 28, MBP was influenced by water availability only with the mix where it was 30% lower at − 1.700 MPa than at − 0.078 MPa. On both days, MBP was between 50% and twofold higher with barley and two to threefold higher with the mix compared with the control. Available N on days 14 and 28 was about twofold higher at − 1.700 MPa than at − 0.078 MPa (Fig. 4e). Compared with the control, available N on day 14 was similar with barley and about twofold higher with the mix at 1.700 MPa and − 0.078 MPa. But residue treatments differed a little in available N at − 0.320 MPa. Available N on day 28 was twofold higher with the mix than the control at − 1.700 MPa, but the two treatments did not differ in available N at higher water availability. Available N on day 28 was about 20% higher in the control than with barley. In all residue treatments and both sampling days, MBN increased with water availability (Fig. 4f). It was about threefold higher at − 0.078 MPa than at − 1.700 MPa. Compared with the control, MBN was about twofold higher with barley and threefold higher with the mix.

4 Discussion

Based on the results of this experiment, Hypothesis 1 (soil respiration, microbial biomass, and P pools are greater at high (− 0.078 MPa) than low (− 1.700 MPa) water availability, due to higher water and substrate availability) can be confirmed. Hypothesis 2 (the difference in soil respiration, microbial biomass, and P pools between high (− 0.078 MPa) and low (− 1.700 MPa) water availability will be greater with low C/P residue than one with high C/P ratio) can only be confirmed for some sampling times and measured parameters.

Soil water availability had a stronger effect on cumulative respiration, available N, and MBN in the mix than the control or barley. The effect of water availability on P pools was smaller than that on respiration, available N, and MBN probably because of flux of P among P pools. Depletion of a given P pool, particularly available P, and MBP triggers the release of P from other pools including citrate and HCl-P and possibly pools not assessed by the Deluca method. Compared with − 0.078 MPa, the low water availability at − 1.700 MPa will result in thinner water films around aggregates and disruption of pore continuity (Tecon and Or 2017). This will restrict substrate diffusion and also diffusion of enzymes away from microbial cells (Geisseler et al. 2012). The restricted diffusion will have a greater impact on substrate availability when

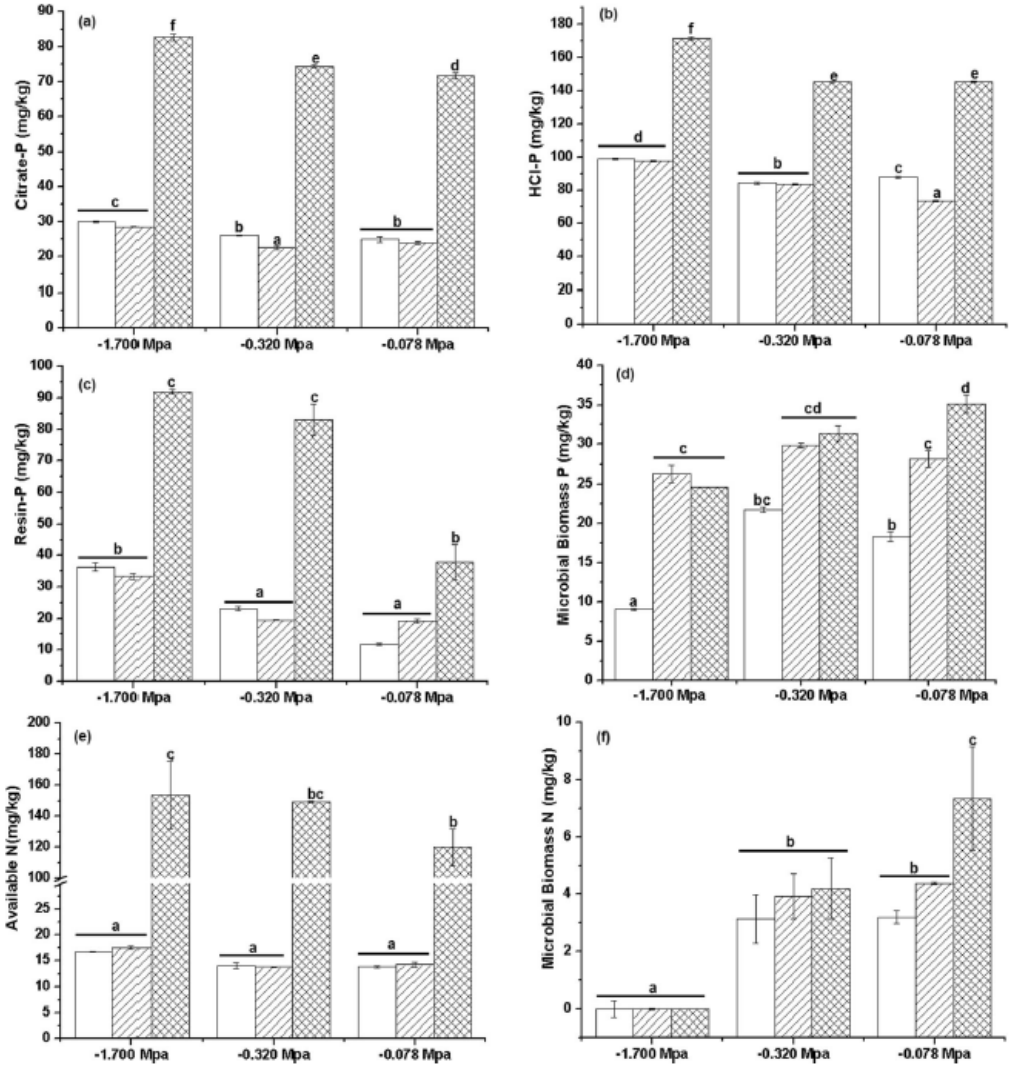

Fig. 3 Citrate-P (**a**), HCl-P (**b**), resin-P (**c**), microbial biomass P (**d**), available N (**e**), and microbial biomass N (**f**) (mg kg^{-1}) 1 day after drying to different water availabilities (− 0.078, − 0.320, and − 1.700 MPa) in control ☐, detritusphere soil of barley straw ▨ and barley straw + faba bean residue (ratio 0.75:0.25) ▩. Columns with different letters are significantly different ($P \geq 0.05$, $n = 4$)

substrate supply is high at − 0.078 MPa as in the mix. During the 2 weeks of detritusphere generation, only 0.9 g of barley straw had been decomposed compared with 1.5 g of the mix, and cumulative respiration during this time was twofold higher with the mix than with barley. Mass loss during detritusphere generation was not only due to CO_2 release but also diffusion of water-soluble compounds into the detritusphere, particularly with the mix. Small residue particles that fell through the mesh may also contribute to the mass loss. Due to the high C/N ratio and complex nature of organic C of mature barley straw, any barley residue particles that had fallen through the mesh would have been more difficult to decompose than faba bean residues from the mix. Therefore, substrate availability in barley detritusphere soil was lower than in the detritusphere of the mix. Available N, MBN, and P pools were up to two or more fold greater with the mix than barley although the C/N and C/P ratio differed little (C/N 95 and 74, C/P 250 and 200, respectively). This suggests that presence of a small proportion of easily decomposable faba bean residue induced a priming effect of both barley residue and native organic matter (Stewart et al. 2015), particularly at high water availability. It is also possible that the presence of sustained C source from barley enhanced respiration and thus decomposition of faba bean residues. With barley and the

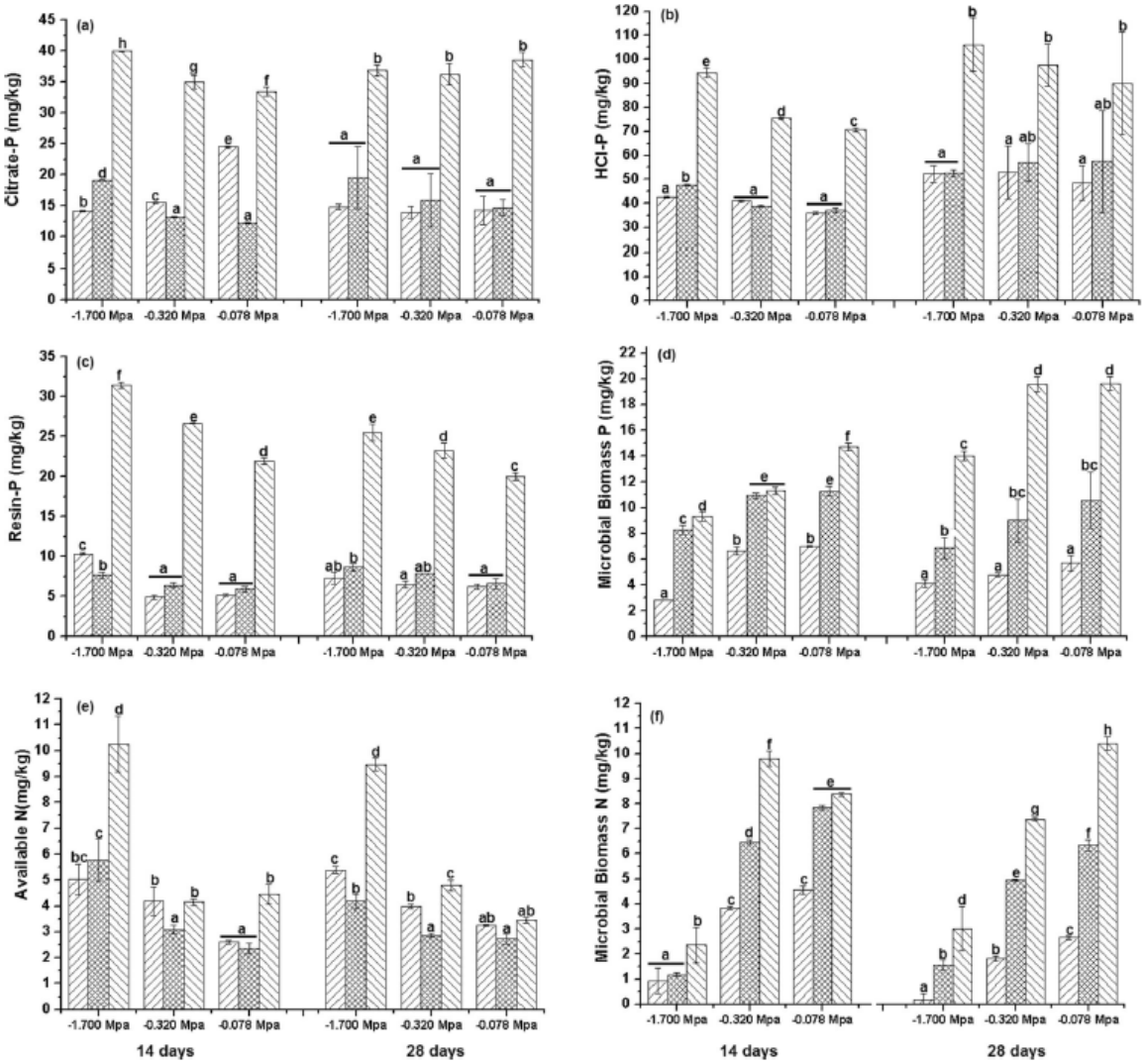

Fig. 4 Citrate-P (**a**), HCl-P (**b**), resin-P (**c**), microbial biomass P (**d**), available N (**e**), and microbial biomass N (**f**) (mg kg^{-1}) after 14- and 28-day incubation at different water availabilities (− 0.078, − 0.320, and − 1.700 MPa) in control ▨, detritusphere soil of barley straw ▩ and barley straw + faba bean residue (ratio 0.75:0.25) ▧. For each sampling time separately, columns with different letters are significantly different ($P \geq 0.05$, $n = 4$)

control, it is likely that substrate availability limited microbial activity even at high water availability and a reduction in water availability had little effect on the measured parameters. With the mix, the higher substrate availability − 0.078 MPa compared with − 1.700 MPa led to higher MBN and MBP which, in turn, resulted in lower available N and resin-P. Differences between − 0.320 MPa and the other two water availabilities only occurred with the mix. This suggests that only with high substrate supply the measured parameters are influenced by small changes in water availability. The higher resin-P, citrate-P, HCl-P, and available N at − 1.700 MPa could also be due to chemical processes induced by drying or by extraction for analysis. Drying can increase P extractability, possibly due to disruption of aluminium-phosphate complexes (Erich and Hoskins 2011) or by inducing death and lysis of microbial cells due to desiccation (Miller et al. 2005; Schimel et al. 2007). Addition of an extractant to the dry soil can cause cell lysis (Turner et al. 2003) and disruption of soil aggregates which exposes additional organic matter and clay surfaces similar to the effect of rapid rewetting of dry soil (Erich and Hoskins 2011; Wang et al. 2014). The latter could increase extractability of P bound to soil particles. The low

MBN and MBP at − 1.700 MPa may therefore be due not only to low in situ microbial biomass but also to cell lysis induced during extraction for analysis.

The higher P concentration in the mix compared to barley induced higher citrate-P, HCl-P, and resin P at all sampling times. MBP on the other hand differed a little between mix and barley 1 day after adjustment of water availability. This suggests that microbes had not yet been able to take up P released from the mix within 1 day even at high water availability. Later however, P released during the decomposition of the mix resulted in higher MBP than with barley.

Available N, MBN, and P pools were lower after 14 and 28 days than after 1 day. This may be due to the conversion of available N into microbial metabolites, microbial biomass turnover; and for P, conversion into P pools not measured by the Deluca method, i.e. more stable, not directly biologically available. Relative differences between residue and water availability treatments were similar at all sampling times for available N and MBN, resin P, and MBP. But for citrate-P and HCl-P, treatment differences that occurred on day one had disappeared on day 28, probably due to the flux of P between these and more stable P pools.

5 Conclusion

This study showed that low water availability limited microbial activity and nutrient supply with high substrate supply, however, had little effect when substrate supply was low even at high water availability. This suggests that low soil water content will have a stronger negative impact on nutrient release in the detritusphere of nutrient-rich residues than of nutrient-poor residues.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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Chapter 4. Influence of N and P addition on soil P pools in barley detritusphere.

P pools in barley detritusphere are influenced by N and P addition to the soil.

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ORIGINAL PAPER

P Pools in Barley Detritusphere Are Influenced by N and P Addition to the Soil

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Abstract
The aim of this experiment was to determine the effect of soil amendment with inorganic N and P on nutrient availability in the detritusphere of low N and P crop residue. To a loamy sand (50% water holding capacity) without fertiliser, with inorganic N or P or both were added and then filled into two PVC caps incubated without (S N, S+P or S+NP) or with barley straw (10 g kg^{-1}; B+N, B+P or B+NP). The open ends of the two PVC caps were covered by fine mesh. For barley treatments, barley straw was placed between the meshes. The open ends of the two PVC caps were pressed together and held tightly with rubber bands. Unamended control had no straw between the caps. After 14 and 28 days of moist incubation, soil at 0–1 mm distance from the surface (detritusphere) was collected. Compared to inorganic treatments alone and the unamended control, P pools and available P and available N in the barley detritusphere were lower whereas microbial biomass P and N were higher. In soil with inorganic P, the decrease of citrate P, HCl-P and resin P in barley detritusphere relative to soil only was greater than without P, but the increase in MBP was not affected by P addition. Microbes in this soil had a limited capacity to accumulate P, likely due to the spatial separation of soil and residues. P released from citrate P, HCl-P and resin P in detritusphere may have been transferred into the residues.

Keywords C/N ratio · C/P ratio · Detritusphere · Nutrient mineralisation · P pools

1 Introduction

The effect of addition of organic soil amendments such as crop residues has been extensively studied. Nutrient availability after the addition of organic amendments depends on their nutrient concentration. For example, crop residue with C/N > 25 and C/P > 200 induce temporary net nutrient immobilisation (Trinsoutrot et al. 2000; Alamgir et al. 2012; Chen et al. 2014).

Addition of inorganic fertilisers to soil amended with crop residues, particularly crop residue with low decomposability (high C/nutrient ratio) can enhance decomposition rate and nutrient availability (Hadas et al. 2004; Nguyen and Marschner 2017), suggesting that microbes decomposing the residue can also take up inorganic N and P added to soil. For example, inorganic N or P addition to soil amended with high C/N residue enhanced decomposition rate (Kranabetter et al. 2005; Li et al. 2017). Nguyen and Marschner (2017) added inorganic N and P to residues with low N and P concentration and then mixed the residues into soil. They found that nutrient additions enhanced soil respiration and microbial biomass compared with the original residues. Organic soil amendments can be a nutrient source for plants, but nutrient release is difficult to predict. The combination of organic and inorganic fertilisers has many advantages, such as increasing productivity, reducing chemical fertiliser consumption and protecting the environment (Moreno-Cornejo et al. 2017; Ara et al. 2018; Zhang et al. 2018).

The detritusphere is defined as a thin layer of soil, within < 5 mm from the decomposing organic amendment and is influenced by amendment decomposition (Liu et al. 2011). The detritusphere has higher concentrations of easily available compounds than bulk soil. In the field, the detritusphere can occur under a crop residue layer on the soil surface or around patches of organic amendments in the soil. Compared with bulk soil, detritusphere soil has higher C and N turnover (Kandeler et al. 1999) and abundance of bacteria and fungi

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(Marschner et al. 2012). In a previous study (Erinle et al. 2018), nutrient availability in detritusphere of barley straw with high C/nutrient ratio was lower or similar to that of the unamended control.

In most studies on inorganic N and P addition to soil amended with plant residues, the residues were mixed into the soil. Little is known about the effect of N and P additions on nutrient availability in the detritusphere of high C/nutrient crop residue. In this study, inorganic N and P were added to soil to reduce the C/N (95) and C/P (255) ratios of the mature barley straw to those of white lupin shoot (C/N 13, C/P 133) which increased soil P pools in the study of Alamgir et al. (2012). The aim of the experiment was to determine the effect of the addition of inorganic N and P, alone or in combination, on P availability and the P pools in barley detritusphere. We hypothesised that (1) compared with bulk soil, the reduction in P pools in barley detritusphere is greater with P added than without P addition whereas microbial biomass P is higher and (2) N addition to soil will increase the effect of P addition compared with P only P added.

2 Materials and Methods

2.1 Soil

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 short, heavy rainfall events. The soil is chromosol according to Australian soil classification and classified as Rhodoxeralf according to US Soil Taxonomy. Soil collection was carried out as described in Erinle et al. (2018). The soil was dried at 40 °C and passed through a 2-mm sieve. The properties of the soil are as follows: pH 6.8 (1:5 soil/water); clay 25%; sand 37%; silt 38%; total P 302 mg kg^{-1}; EC (1:5) 0.1 dS m^{-1}, total organic C 17 g kg^{-1}, total organic N 1.5 g kg^{-1}, bulk density 1.3 g cm^{-3} and maximum water holding capacity (WHC) 349 g kg^{-1}.

2.2 Residue

Mature barley straw (*Hordeum vulgare* L.) was used because in our previous study (Erinle et al. 2018), nutrient availability in its detritusphere was lower or similar to that of the unamended control. After drying in a fan-forced oven at 40 °C, the barley straw was ground and sieved to 0.25–2 mm particle size. Barley straw properties are total organic C 408 g kg^{-1}, total N 4.3 g kg^{-1}, total P 1.7 g kg^{-1}; water extractable P 0.1 g kg^{-1}; C/N ratio 95 and C/P ratio 255.

2.3 Experimental Design

The microcosms used to generate detritusphere soil are described in Erinle et al. (2018). Soils were 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. After 7 days incubation, inorganic N (4.36 g $KNO_3 \cdot kg^{-1}$ soil), P (0.15 g $KH_2PO_4 \cdot kg^{-1}$ soil) or both were thoroughly mixed into the moist soil and 100 g soil (dry weight basis) was filled into caps of PVC tubes (height 20 mm, diameter 70 mm) and packed to a bulk density of 1.3 g cm^{-1}. Fine nylon mesh (0.1 mm × 0.8 mm) was cut into 85-mm diameter circles and placed over the soil to cover the open side of each cap. Ground barley straw (2.0 g per two cups, equivalent to 10 g kg^{-1}) was placed between two layers of mesh covering the entire soil surface. Then, the open ends of the two caps were pressed together which were held in place with rubber bands. Addition of inorganic N and P reduced the C/N and C/P ratios of the barley straw to those of rapidly decomposing white lupin (C/N 13; C/P 133; Alamgir et al. 2012). There were eight treatments with three replicates each, unamended control (Co), soil with inorganic N (S+N), inorganic P (S+P) or both inorganic N and P (S+NP), detritusphere of barley alone (B), barley with inorganic N (B+N), inorganic P (B+P) or both inorganic N and P (B+NP). The microcosms were incubated at 20–25 °C in the dark and kept at 50% WHC for 2 or 4 weeks. To collect detritusphere soil for analyses, the two PVC caps were separated from each other and the two layers of mesh with the residues was removed. Soil at 0–1 mm distance from the surface was collected. For each replicate, soil from both sides of the mesh was combined and analysed for microbial biomass N and P, N and P availability and P pools.

2.4 Analyses

Soil analyses were carried out as described in Erinle et al. (2018). Briefly, soil maximum water holding capacity was measured at 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 (Rayment and Higginson 1992). Total organic C of soil was determined by wet oxidation after Walkley and Black (1934). Total N in soil and plant residues was determined using 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).

For determination of soil P pools the method of DeLuca et al. (2015) was modified because in previous studies, two of the pools, $CaCl_2$ P and phosphatase P, were variable and low. P pools extracted were active inorganic P pool sorbed to clay

particles or weakly bound in inorganic precipitates (10 mM citric acid) and soluble, active and moderately stable inorganic P adsorbed to mineral surfaces or present in inorganic precipitates (1 M HCl). Each pool was measured in parallel by shaking 0.5 g of soil with 10 ml of extractant for 3 h on an end-over-end shaker. Two additional P pools were included. Resin (available) 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 (630 nm) using the malachite-green method as described in Ohno and Zibilske (1991). MBP is the difference in P concentration between fumigated and non-fumigated soil (Kouno et al. 1995). Available N (ammonium and nitrate) 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 according to Miranda et al. (2001). Available N is the sum of ammonium and nitrate N. 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. A proportionality factor of 0.57 was used to convert ammonium to MBN (Moore et al. 2000).

2.5 Statistical Analysis

Data of microbial biomass, N and P availability and P pools was log10 transformed to achieve normal distribution of the residuals. Then the data was analysed by one-way analysis of variance (ANOVA). For each sampling time separately, Tukey's multiple comparison test was used to separate among means, where fixed factors had significant effects ($P \geq 0.05$). The statistical analyses were carried out in Genstat v18.2 (VSN International Ltd., UK).

3 Results

After 14 days, dry weight of barley straw was about 30% lower than initially in barley alone (B) and barley with P (B+P), but only about 25% lower in barley with N (B+N) and barley with N and P (B+NP) (Table 1). On day 28, straw dry weight was reduced by about 10% in all treatments compared with day 14.

At both sampling times, citrate P, HCl-P and resin P differed little among treatments with barley (B, B+N, B+P, B+NP). Citrate P on day 14 was highest in soil with P (S+P) and lowest in B+P (Fig. 1a). Citrate P was lower in barley treatments than in the control, but was higher than in the control in S+P. Citrate P was about 20% lower than in the control with barley alone (B). Citrate P was 25% lower in B+N than in S+N, 50% lower in B+P than in S+P and 15% lower in B+NP than in S+NP. On day 28, citrate P was highest in soil with N and P (S+NP) where it was between 50% and two-fold higher than the other treatments which did not differ.

Table 1 Dry weight of barley straw remaining after 2 and 4 weeks (initial weight = 2.0 g) in barley straw alone (B) or barley + N (B+N), + P (B+P) or + N and P (B+NP). For each sampling time separately, different letters indicate significant differences ($n = 4$; $P \leq 0.05$)

Treatments	14 days	28 days
B	1.34[a]	1.23[a]
B+N	1.44[b]	1.31[b]
B+P	1.40[a]	1.25[a]
B+NP	1.46[b]	1.35[b]

On day 14, HCl-P compared with the control was about 10% higher in S+P and S+NP, but between 10 and 15% lower in the other treatments (Fig. 1b). Barley alone reduced HCl-P by about 15% compared with the control. HCl-P was about 15% lower in B+N than in S+N and about 25% lower in B+P than in S+P and 10% lower in B+NP than in S+NP. HCl-P on day 28 was higher in the control and S+NP than the other treatments. With inorganic nutrient addition in soil, HCl-P increased in the following order: S+N > S+P > S+NP. Barley treatments did not differ in HCl-P which was about 25% lower than in the control. HCl-P was 10% lower in B+N than in S+N, 20% lower in B+P than in S+P and 25% lower in B+NP than in S+NP.

Resin P on day 14 was higher than in the control only in S+P where it was about 25% higher (Fig. 1c). Compared with the control, resin P was about 10% lower in S+N and S+NP. In all barley treatments, resin P was about 50% lower than in the control. Barley alone reduced resin P by about 60% compared with the control. With N and P addition, resin P was about 50% lower in treatments with barley compared with the soil without residues. On day 28, resin P was about 10% higher than in the control in S+P and S+NP, but did not differ from the control in the other treatments except for B+P where it was 25% lower. Barley addition did not influence resin P without nutrient addition or with N compared with respective treatments without barley (Co and S+N). Resin P was about 50% lower in B+P than in S+P and 40% lower in B+NP than in S+NP.

MBP on day 14 was highest in barley alone where it was two-fold higher than in the control (Fig. 1d). It was about 75% higher than in the control in the other barley treatments, but only 10% higher in S+N and S+NP. MBP was about 25% higher in B+N than in S+N and in B+NP than in S+NP, but it was nearly two-fold higher in B+P than in S+P. On day 28, MBP was higher than in the control only in barley treatments. MBP was about 40% higher in B than in the control and in B+NP than in S+NP, but 15% higher in B+N than in S+N and 75% higher in B+P than in S+P.

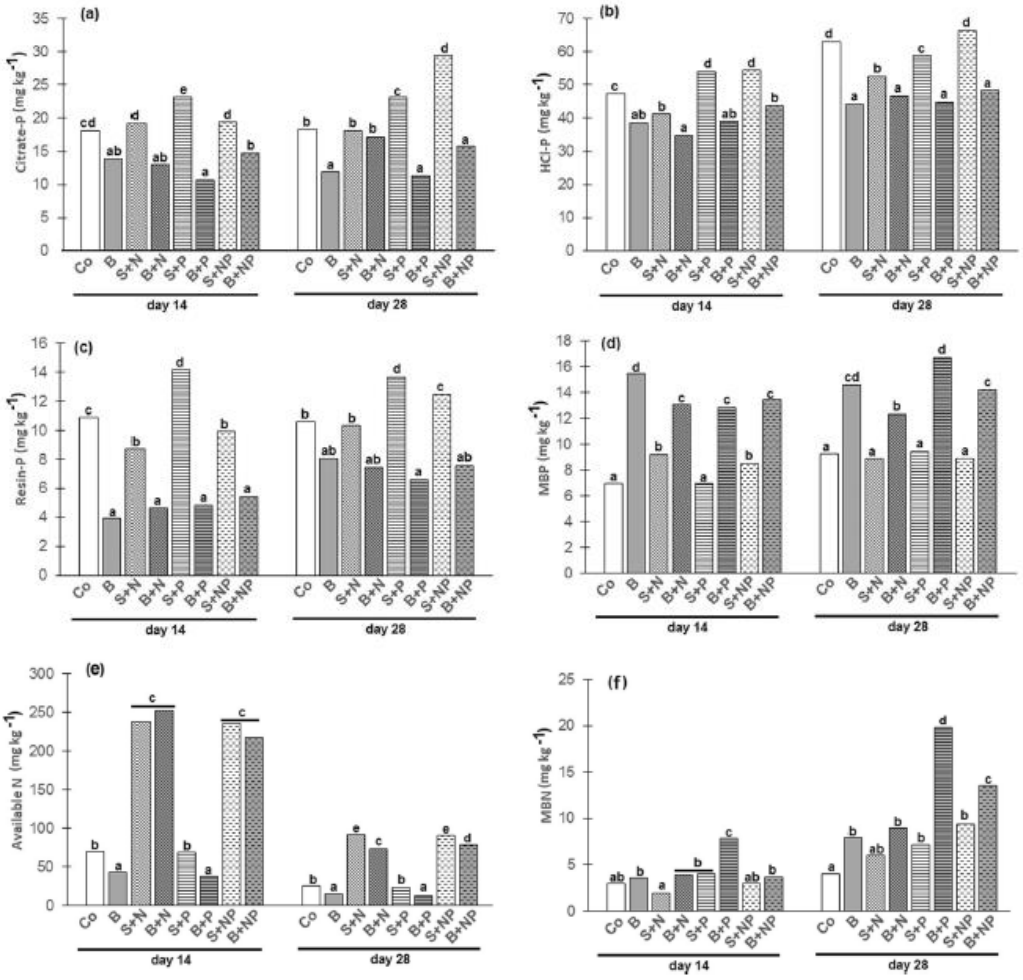

Fig. 1 Citrate P (**a**), HCl-P (**b**), resin P (**c**), microbial biomass P (**d**), Available N (**e**) and microbial biomass N (**f**) in soil mixed with inorganic N, P, or their combination, in unamended control (Co) or soil (S)+N, + P or + NP and detritusphere of original barley straw (B) with reduced C/N (B+N) or C/P (B+P) ratios or combination of both (B+NP) after 14 and 28 days ($n = 4$). Different letters indicate significant differences between treatments based on log10 transformed data ($P \leq 0.05$)

Available N on day 14 was about five-fold higher in treatments with N addition (S+N, B+N, S+NP, B+NP) than the other treatments which differed little in available N (Fig. 1e). Barley alone reduced available N by about 15%, compared with the control and in B+P compared with S+P, but had no effect on available N when N was added (B+N, B+NP). Available N was about 75% lower on day 28 than on day 14 in all treatments. Barley reduced available N by about 20% compared with soil alone in all treatments.

On day 14, MBN was higher than in the control only in B+P where it was about two-fold higher. MBN increased about two-fold from day 14 to day 28. On day 28, MBN was about five-fold higher in B+P than in the control. MBN was also higher than in the control in all other treatments except S+N (Fig. 1f). MBN was about two-fold higher in barley alone than in the control and in B+P than in S+P, but only 30% higher in B+NP than in S+NP. Barley addition had no effect on MBN with N addition.

4 Discussion

In most previous studies which showed that organic soil amendments with high C/nutrient ratio can reduce nutrient availability compared with unamended soil, the amendments were mixed into the soil (e.g. Trinsoutrot et al. 2000; Alamgir et al. 2012; Chen et al. 2014). In these experiments, soil microbes were in direct contact with residue particles, colonising the particle surfaces and immobilising mineralised N and P. In the current study, direct contact of soil microbes and residue

particles was limited to the few residue particles that fell through the mesh. The observed effects of residues on P pools, available N and MBN and MBP in the detritusphere can be explained by several processes: (i) transfer of N and P from the soil into the residues by fungal hyphae, (ii) diffusion of nutrients from soil to residues induced by N and P depletion in the residues and (iii) transfer of organic acid anions from the residues into the soil. Frey et al. (2003) showed that N can be transferred from soil to an overlying layer of high C/N residues. P can move from source to sink in hyphae of mycorrhiza (Johri et al. 2015). This may also occur via fungal hyphae growing across the detritusphere interface. Decomposition of high C/nutrient residues induces net N and P immobilisation in the microbial biomass (Trinsoutrot et al. 2000, Alamgir et al. 2012). This depletion of available N and P by microbes in the residue layer may have increased diffusion of N and P from the soil. The higher MBP and MBN in the detritusphere than in the bulk soil indicates that microbial growth was stimulated either by residue particles that passed through the mesh, soluble C compounds from the residues or C transferred from residues into the soil by fungal hyphae (Frey et al. 2003). Citrate and HCl-P may have been reduced in barley detritusphere by organic acid anions or protons produced during straw decomposition (Singh and Amberger 1998; Kumari et al. 2008).

The first hypothesis (compared with bulk soil the reduction in P pools in barley detritusphere is greater with P added than without P addition whereas microbial biomass P is higher) can be confirmed for citrate P, HCl-P and resin P, but not for MBP. The increase in MBP compared with bulk soil was smaller with added P than with P addition on day 14 and not affected by P addition on day 28. The concentration of citrate P, HCl-P and resin P in the detritusphere differed little among treatments even when P was added. This indicates that the concentration represents the minimum values to which these P pools can be decreased over 4 weeks in the presence of barley residues. Addition of P to bulk soil increased citrate P, HCl-P and resin P compared with unamended soil. Therefore the reduction of N the detritusphere compared with bulk soil was greater in treatments with P added than without P. On day 28, the decrease in resin P in barley detritusphere was accompanied by an increase in MBP suggesting that resin P was taken up by microbes. However, the reduction in citrate and HCl-P was greater than the increase in MBP indicating that P from these pools was not taken up by microbes in the detritusphere. P from these pools may have been transferred to the residues or transformed to soil P pools in the detritusphere not assessed by the Deluca method such as stable organic P (e.g. microbial metabolites) or stable inorganic P (e.g. NaOH soluble P).

Soil microbes can accumulate P in the form of polyphosphates (Buenemann et al. 2008). Therefore, we hypothesised that MBP would be increased to a greater extent compared with bulk soil in treatments with P than without P addition. However, this was not the case. This suggests that microbes in this soil have a limited capacity to accumulate P, MBP was optimal even without P addition, or that P uptake was limited by another factor such as availability of decomposable organic C due to the spatial separation of residues and detritusphere soil.

On day 14, the presence of straw also reduced available N, but only in treatments where N was not added to the soil. Apparently, available N was too high in treatments with N addition to be significantly reduced by immobilisation. The reduction of available N with straw from day 14 to day 28 was accompanied by an increase in MBN suggesting an increase in microbial N uptake over time. In contrast, MBP changed little over time suggesting that P uptake by microbes was already maximal on day 14.

The second hypothesis (N addition to soil will increase the effect of P addition compared with P only P added) has to be declined. The hypothesis was based on the assumption that decomposition of barley straw would be limited by both N and P. However, addition of N together with P had little effect on P pools compared with the treatment with only P added. This suggests that N was not limiting microbial growth which is corroborated by the similar MBN in unamended soil and treatments with N added.

5 Conclusion

Addition of P increased the concentration of citrate P, HCl-P and resin P in bulk soil, but their concentration in detritusphere soil was not affected by P addition. This suggests that the detritusphere concentrations represent minimum values for these pools in this soil when in contact with decomposing barley straw. The reduction of citrate P, HCl-P and resin P in detritusphere soil compared with bulk soil was greater with P addition than without, but microbial biomass P was little affected by P addition. This indicates that microbes had a limited capacity to accumulate P, likely due to the spatial separation of soil and residues. P released from citrate P, HCl-P and resin P in detritusphere may have been transferred to the residues. Experiments with ^{32}P labelled fertiliser would be necessary to track the fate of added P in soil and residues.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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Chapter 5. Changes in P pools in the detritusphere: influence of P removal or switch of residues with low and high C/P ratio.

Changes in phosphorus pools in the detritusphere induced by removal of P or switch of residues with low and high C/P ratio.

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ORIGINAL PAPER

Changes in phosphorus pools in the detritusphere induced by removal of P or switch of residues with low and high C/P ratio

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Abstract
The effect of the addition of crop residues to soil has been extensively studied; however, little is known about their effect on P pools in the detritusphere and how these pools change if the residue is replaced by another residue with similar or different P concentration. An experiment was conducted to determine the influence of a change of residue types on P pools in the detritusphere. Detritusphere soil was generated by placing 20 g kg^{-1} of either mature barley straw (H; high C/P 255) or young faba bean residue (L; low C/P 38) between two fine nylon meshes which were then sandwiched between two PVC caps filled with loamy sand maintained at 50% water holding capacity throughout the experiment. Then, the open ends of the caps were pressed together and held in place with rubber bands. After 2 weeks of moist incubation, the residues were replaced with either a H or L, resulting in four residue treatments: high-high (HH), high-low (HL), low-low (LL), or low-high (LH) which were incubated another 14 days. A control without residues between the caps was unamended throughout. The following P pools were measured in soil at 0–1 mm from the surface 14 days after the first (day 14) and second (day 28) residue addition: readily available P ($CaCl_2$ and anion exchange P); P bound to soil particles (citrate and HCl-P); and microbial biomass P (MBP). On day 14, P pools and available N were higher, but MBP and microbial biomass N (MBN) were lower in L than in H. On day 28, P pools and available N followed the order LL > HL > LH > HH, whereas MBN and MBP were highest in HL. In a second experiment, the effect of crop residue removal and replacement with anion exchange membrane (AEM) on P pools in the detritusphere was assessed. Detritusphere soil was generated using faba bean residue as described above. The control had no residues between the caps. After 2-week moist incubation, the residues and the meshes were removed and either replaced with three AEM strips (approximately 6 × 2 cm each) or left without AEM. The strips were replaced every 2 days for 2 weeks. P sorbed to the strips (AEM-P) was determined after removal. After 1 and 2 weeks, bioavailable P pools were measured. Removal of P by AEM decreased most P pools in faba bean detritusphere. This study showed that within 14 days, P pools in the detritusphere are influenced by P supply and P removal and that a change in the C/P ratio of added residue can either decrease or increase concentrations of various soil P pools.

Keywords C/nutrient ratio · Detritusphere · Nutrient availability · Residues

Introduction

In soil, phosphorus (P) exists in various pools (Guo and Yost 1998), including labile, non-labile and stable P pools (Cherubin et al. 2016). Soil solution P represents a small proportion of total P (< 0.1%), but is the reservoir for P uptake by plants and microorganisms (Schachtman et al. 1998; Kruse et al. 2015). A decrease in the soil solution P concentration results in the release of P from the labile P pool.

Nutrient availability after the addition of organic amendments depends on their nutrient concentration. The C/P ratio of organic amendments such as crop residues influences P availability and P pools of the surrounding soil (Dalal 1979). Mixing soil with crop residues with a $C/P > 200$ induces net P immobilization and depletion of P pools, whereas residues with lower C/P ratios increase P availability and labile P pools (Alamgir et al. 2012). For example, mixing soil with a low C/P residue increased the labile P pools 2- to 6-fold compared to amendment with a high C/P residue (Nziguheba et al. 2000; Alamgir and Marschner 2013a). In soil mixed twice with

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residues, when a low C/nutrient residue was followed by a high C/nutrient residue, N and P availability were lower than when a low C/nutrient residue was mixed into previously unamended soil (Marschner et al. 2015). When low C/P residue followed high C/P residue, nutrients mineralised by the low C/P residue were rapidly immobilised by microbes decomposing the previously added high C/P residue, reducing nutrient availability compared to low C/P residue added alone. In contrast, when high C/P residue followed low C/P residue, nutrients mineralised by decomposition of the previously added low C/P residue together with the freshly added high C/P residue led to higher nutrient availability than with high C/P residue alone. This so-called legacy effect is defined as the influence of a previous residues C/nutrient ratio on microbial activity, biomass and nutrient availability after the addition of a second residue with similar or different C/nutrient ratio (Marschner et al. 2015)

Labile and non-labile P pools can be depleted by plants through uptake (Crews 1996; Guo et al. 2000; Hoang and Marschner 2017) or by application of high C/P residues. Addition of high C/P residues, such as cereal stubble (e.g. barley or wheat straw) may reduce P availability through immobilisation in the microbial biomass (Damon et al. 2014). Hoang and Marschner (2017) found that mixing soil with barley straw (C/P 255) depleted HCl-P and citrate P, but increased phosphatase P, microbial P and $CaCl_2$ P. Alamgir and Marschner (2013b) also reported that HCl-P decreased by up to 30% after the amendment with high C/P residues. Less labile P pools such as HCl-P may be accessed by plants or microbes either directly or indirectly. Indirect access via depletion of labile P pools can trigger the release of P from HCl-P pools as well as P from non-occluded sites on Fe and Al hydroxides (citrate P) (Crews 1996).

The detritusphere is defined as thin layer of soil (generally < 5 mm) directly adjacent to plant litter and is influenced by residue decomposition (Liu et al. 2011). It is considered to be one of the three hotspots in the soil, the other two being the rhizosphere and biopores (Kuzyakov and Blagodatskaya 2015). In the field, detritusphere would occur, for example, under a litter or crop residue layer on the soil surface or around patches of residues in the soil. Soil disturbance could disrupt detritusphere formation or remove or dilute the detritusphere effect. Nutrient availability is higher in the detritusphere than in the bulk soil. For example, de Neergaard and Magid (2015) and Ha et al. (2007) found higher available P concentration in the detritusphere of some crop residues than in the control and Kandeler et al. (1999) reported increased N turnover in the detritusphere compared to bulk soil.

As outlined above, the effect of residue C/P ratio on P pools has been studied (Alamgir et al. 2012; Alamgir and Marschner 2013a; Damon et al. 2014; de Neergaard and Magid 2015); however, less is known about the response of P pools to P removal or addition in the detritusphere. The detritusphere offers the unique possibility to apply residues multiple times without soil disturbance. For example, residue can be applied to the soil surface, left for a period of time to induce a detritusphere and then removed and replaced by the following residue.

Two experiments were conducted in this study. Using crop residues with either high or low C/P ratio, the aim of the first experiment was to determine the effect of replacement of one residue with another on detritusphere P pools without soil disturbance. A similar situation may occur in the field when surface litter of one species is removed by wind or machinery (e.g. baling) and replaced by the residue of another species. To further investigate the effect of P removal from the detritusphere soil without soil disturbance, a second experiment was carried out using anion exchange resin strips to remove P similar to P removal by microbes decomposing high C/P residue. P pools were determined using four different extractants: $CaCl_2$ (soluble P), phosphatase (enzyme extractable organic P), citric acid (citrate extractable P) and HCl (mineral occluded P) (DeLuca et al. 2015). These pools are considered to be biologically available because the extractants mimic mechanisms by which plants and microbes acquire P. The first hypothesis was that P pools will change depending on the order in which the residues are placed; when low C/P residue follows high C/P residue, measured parameters will be lower than with low C/P residue added twice, but when high C/P residue application follows low C/P residue, measured parameters will be higher than with high C/P residue added twice. This hypothesis is based on the legacy effect described in Marschner et al. (2015) where residues were mixed into soil. But the present experiment differed from Marschner et al. (2015) because the residues were not mixed into the soil and the first residue was removed before the second residue was placed on the soil surface. It is not known if and to what extent the C/P ratio of the first residue influences P pools after its removal. The second hypothesis was that the reduction in P pools induced by high C/P following low C/P residue can be mimicked by placement of anion exchange membranes on the detritusphere of low C/P residue.

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 has a Mediterranean climate. The soil is classified as a Chromosol (Australian soil classification) or Rhodoxeralf (US Soil Taxonomy). The soil was dried at 40 °C and sieved (< 2 mm). The properties of the soil were pH 6.8 (1:5 soil/water), clay 25%, sand 37%, silt 38%, total P 302 mg kg^{-1}, EC (1:5)

0.1 dS m^{-1}, total organic C 17 g kg^{-1}, total organic N 1.5 g kg^{-1}, bulk density 1.3 g cm^{-3} and maximum water-holding capacity (WHC) 349 g kg^{-1}.

Two types of crop residues were used: the low C/P residue was young faba bean shoot (*Vicia faba* L., C/P 38) and the high C/P residue was mature barley straw (*Hordeum vulgare* L., C/P 255) (Table 1). The residues were dried at 40 °C, ground and sieved to 0.25–2 mm particle size.

Experimental design

The microcosms used to generate detritusphere soil are described in Erinle et al. (2018). Briefly, PVC caps used as end caps of tubes (height 20 mm, diameter 70 mm) were filled with 90 g of dry soil equivalent packed to a bulk density of 1.3 g cm^{-1} so that the soil surface was level with the open side of the caps. The soil was moistened to 50% of WHC and incubated for 7 days at 20–25 °C in the dark before the onset of the experiment. At the end of the pre-incubation, nylon mesh (0.1 mm × 0.8 mm) was cut into circles of 85 mm diameter and placed over the soil on the open side of each cap. Throughout the following incubation, soil water content was maintained at 50% WHC.

The first experiment was carried out with the aim to determine to what extent P pools in the detritusphere are influenced by the C/P ratio of the current and previous residue (Fig. 1). Two crop residues were used, mature barley straw with high C/P ratio (H) as net P sink and young faba bean residue with low C/P ratio (L) as net P source. In a previous study, we found that P pools in the detritusphere soil of faba bean residue were higher than in an unamended soil whereas P pools differed little between control and barley straw detritusphere (Erinle et al. 2018). Faba bean residues or barley straw (3.6 g equivalent to 20 g kg^{-1}) were placed between the two open ends of two caps which were covered by the mesh. After pressing the two open ends together, the residue layer was between two meshes. The two caps were held in place with rubber bands. The control had no residue between the meshes. The microcosms were incubated at 20–25 °C in the dark for 2 weeks. Then, the two caps were separated and the remaining first residue removed from the mesh after which the second residue added without disturbing the soil surface. As after the first residue addition, the two PVC caps were pressed together and incubated at 50% WHC in the dark for 2 weeks. There were four treatments: replacement of the residues with either same residue (H-H or L-L) or the other residue (H-L or L-H). The control remained without residue between the meshes.

Soil analyses were carried out on day 14 and day 28 (before and 2 weeks after the second residue addition). To collect soil for analyses, the two PVC caps were separated from each other, and the two layers of mesh with the residues were removed. Then, detritusphere soil (0–1 mm from the soil surface) was collected. This thin layer was used to maximise the residue effect. For each replicate, soil from both sides of the mesh was combined.

The second experiment was carried out to determine if the reduction of P pools after replacement of low C/P residue by high C/P residue in experiment 1 could be mimicked by using anion exchange membranes as P sink (Fig. 2). The detritusphere was generated with faba bean residue. An unamended control was also included. Barley straw detritusphere was not included because P pools did not differ from the control in experiment 1. After 2 weeks, the two PVC caps were carefully separated from each other. The remaining residue and the two meshes were removed and replaced with three strips of anion exchange membrane (AEM, approximately 6 × 2 cm each) per microcosm, covering the whole soil surface of the open ends. Additional treatments included microcosms without AEM placement after removal of the residue. Then, the two PVC caps were pressed together again. There were four treatments with four replicates each: (i) faba bean detritusphere with AEM, (ii) faba bean detritusphere without AEM, (iii) unamended control with AEM and (iv) unamended control without AEM. To maximise P removal, the AEM strips were replaced every 3 days for 2 weeks. P sorbed on the AEM was measured. At the end of the first and second week, P pools in soil at 0–1 mm distance from the surface were measured.

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

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
C/P ratio	255b	38a
C/N ratio	95b	9a

Measurements

Soil properties were determined as described in Erinle et al. (2018). Briefly, soil maximum water-holding capacity was measured at matric potential − 10 kPa (Wilke 2005). Soil texture was determined by the hydrometer method (Ge and Or 2002). Soil pH was measured in a 1:5 (*w*/*v*) soil to reverse osmosis (RO) water ratio (Rayment and Higginson 1992). Total organic C of soil was determined by wet oxidation according to Walkley and Black (1934). For total P, soil and plant residues were digested with a mixture of HNO_3 and $HClO_4$ followed by P determination in the extract by the phosphovanadomolybdate method (Hanson 1950). Total N

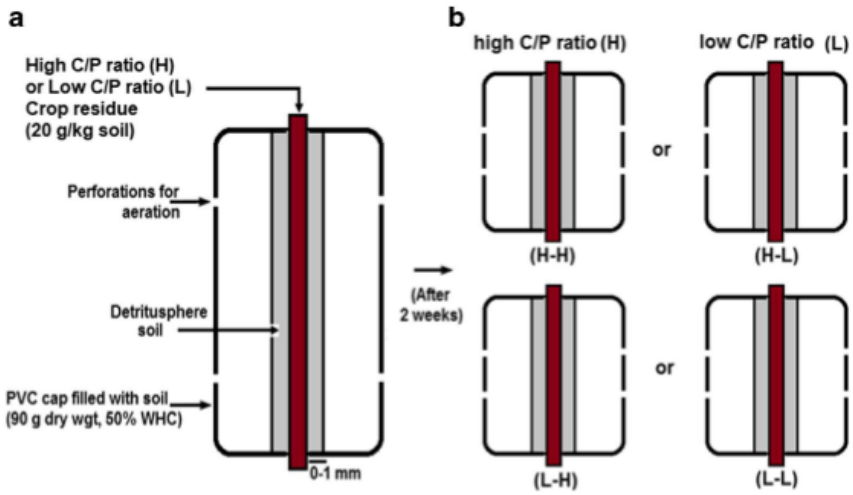

Fig. 1 Schematic diagram of PVC caps used in experiment 1

in soil and plant residues was determined according to McKenzie and Wallace (1954).

Soil P pools were measured as described in DeLuca et al. (2015). They were weakly adsorbed inorganic P (10 mM $CaCl_2$), active inorganic P pool sorbed to clay particles or weakly bound in inorganic precipitates (10 mM citric acid), acid phosphatase labile organic P (0.2 enzyme units phosphatase) and soluble, active and moderately stable inorganic P adsorbed to mineral surfaces or present in inorganic precipitates (1 M HCl). Each pool was extracted separately by shaking 0.5 g of soil with 10 ml of extractant for 3 h on an end-over-end shaker. P in the filtrate was measured at 630 nm with the malachite-green method (Ohno and Zibilske (1991).

In experiment 1, two additional P pools were included: resin (available) P and microbial biomass P (MBP) which were determined with the anion exchange resin method (Kouno et al. 1995). The P concentration was also determined with malachite-green method. MBP is the difference in P concentration between fumigated and un-fumigated soil (Kouno et al. 1995). In this experiment, the term P pools refers to $CaCl_2$ P, phosphatase P, citrate P, HCl P and resin P.

Available N (ammonium and nitrate) was extracted with 2 M KCl in a 1:5 soil extractant ratio placed on an end-over-end shaker for 1 h. Ammonium-N and nitrate-N were determined using the methods of Willis et al. (1996) and Miranda et al. (2001), respectively. 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 ammonium concentration between fumigated and non-fumigated samples divided by 0.57 as suggested by Moore et al. (2000).

In the second experiment, after rinsing the AEM in RO water, 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).

Statistical analysis

To ensure normal distribution of the P pool, resin P, MBP and available N and MBN data for statistical analyses, values were log-transformed (log base 10). In experiment 1, log-transformed data were analysed by two-way ANOVA with unbalanced design using treatments and sampling time as factors. In experiment 2, P pool data was analysed by two-way ANOVA. Data of P extracted from the resin with faba bean and the control were compared pair-wise by Student's *t* test. Tukey's multiple comparison test was used to determine which treatments were significantly different ($P \leq 0.05$). The statistical analyses were carried out in Genstat v18.2 (VSN International Ltd., UK).

Results

Experiment 1

Fourteen days after the first residue addition, P pools and available N were between 5- and 20-fold higher with low C/P faba bean (L) than the control or with high C/P barley (H) (Fig. 3). On day 14, differences between L and the other treatments were greater in labile P pools ($CaCl_2$ P, resin P) and phosphatase P (10- to 40-fold higher with L) than in citrate P and HCl P (6- to 10-fold higher). MBP was about 2-fold higher with H than the control and with L. Available N was 10-fold higher in L than the control and H. MBN was 3 to 4-fold lower in the control than with residues.

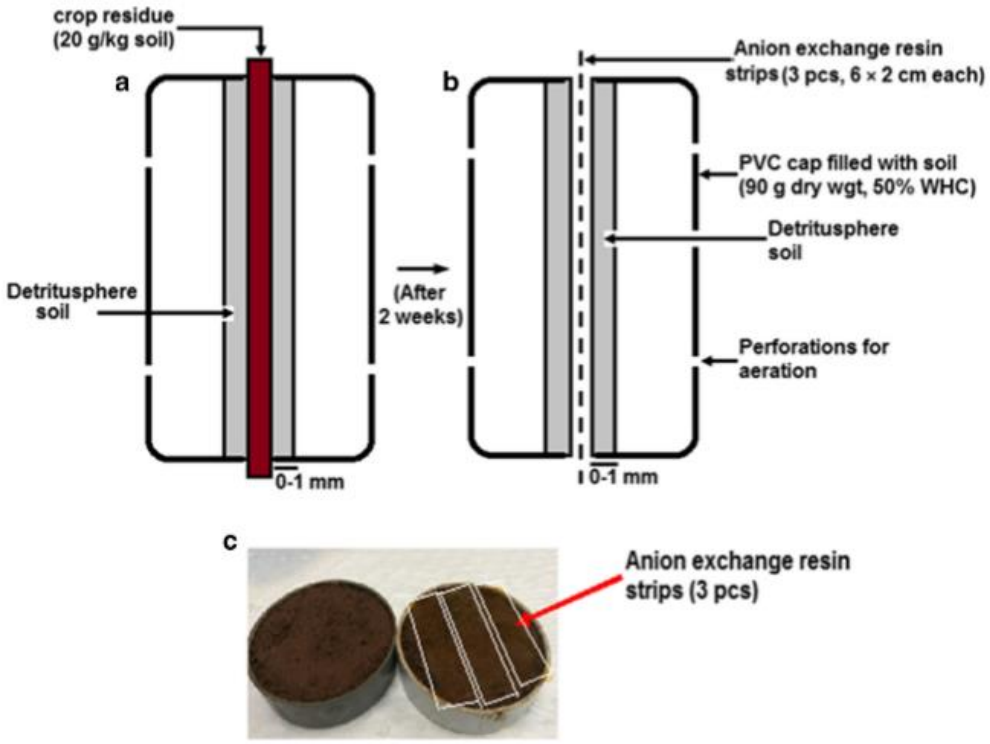

Fig. 2 Schematic diagram of PVC caps used in Experiment 2

On day 28, 14 days after the addition of the second residue, $CaCl_2$ P was lowest in HH. Compared to HH, $CaCl_2$ P was 2-fold higher in the control, about 10-fold higher in HL and LH and 20-fold higher in LL (Fig. 3a). $CaCl_2$ P in the control was 2-fold higher on day 28 than day 14. Compared to H on day 14, $CaCl_2$ P was higher in all residue treatments on day 28, particularly those where L had been added at least once (HL, LH and LL) (Fig. 3). $CaCl_2$ P was similar in L on day 14 and in LH, but compared to L, it was about 10% higher in HL and 2-fold higher in LL. Phosphatase P, citrate P and HCl P on day 28 did not differ between control and HH (Fig. 3b–d). Compared to the control, phosphatase P was 30-fold higher in HL, 10-fold higher in LH and 50-fold higher in LL (Fig. 3b). Phosphatase P, citrate P and HCl P did not change over time in the control and did not differ between H on day 14 and HH on day 28. Compared to L on day 14, phosphatase P was about 50% lower in LH and nearly 2-fold higher in LL. Phosphatase P did not differ between L and HL. Compared to the control, citrate P on day 28 was 2-fold higher in LH, 8-fold higher in HL and 10-fold higher in LL (Fig. 3c). Compared to L on day 14, citrate P was 5-fold lower in LH and 20% higher in LL. HCl P on day 28 was about 3-fold higher in HL, LH and LL than the control (Fig. 3d). HCl P was about 50% higher in LL than LH (Fig. 3d). HCl P in HL, LH and LL on day 28 did not differ from L on day 14. Compared to HH, resin P on day 28 was higher in all other treatments, about 50% in LH, 2-fold in the control, 15-fold in HL and 25-fold in LL (Fig. 3e). Resin P did not differ between H on day 14 and HH on day 28. It increased by about 75% in the control from day 14 to day 28. Compared to L on day 14, resin P was about 10-fold lower in LH, 15% higher in HL and nearly 2-fold higher in LL. MBP on day 28 was lowest in LH (Fig. 3f). Compared to LH, MBP was 2-fold higher in the control, about 6-fold higher in HH and LL and 10-fold higher in HL. MBP on day 28 was higher in most treatments than on day 14 except in LH where it was 3-fold lower than H and 50% lower than L. Compared to H on day 14, MBP was about 2-fold higher in HH and LL and 3-fold higher in HL. MBP in HH, HL and LL was 3 to 5-fold higher than L.

Available N on day 28 was low in the control and HH (Fig. 2g). Compared to the control, available N was 4-fold higher in LH, 50-fold higher in HL and 100-fold higher in LL. Compared to the control and H on day 14, available N on day 28 was about 50% lower in the control and HH, but nearly 2-fold higher in LH and 20 and 30-fold higher in HL and LL. Available N in LH was about 8-fold lower than in L, but it was 2 to 3-fold higher in HL and LL. MBN on day 28 was lowest in the control (Fig. 3h). Compared to the control, MBN was 4-fold higher in HH and LH and about 10-fold higher in HL and LL. MBN did not change over time in the control. It was

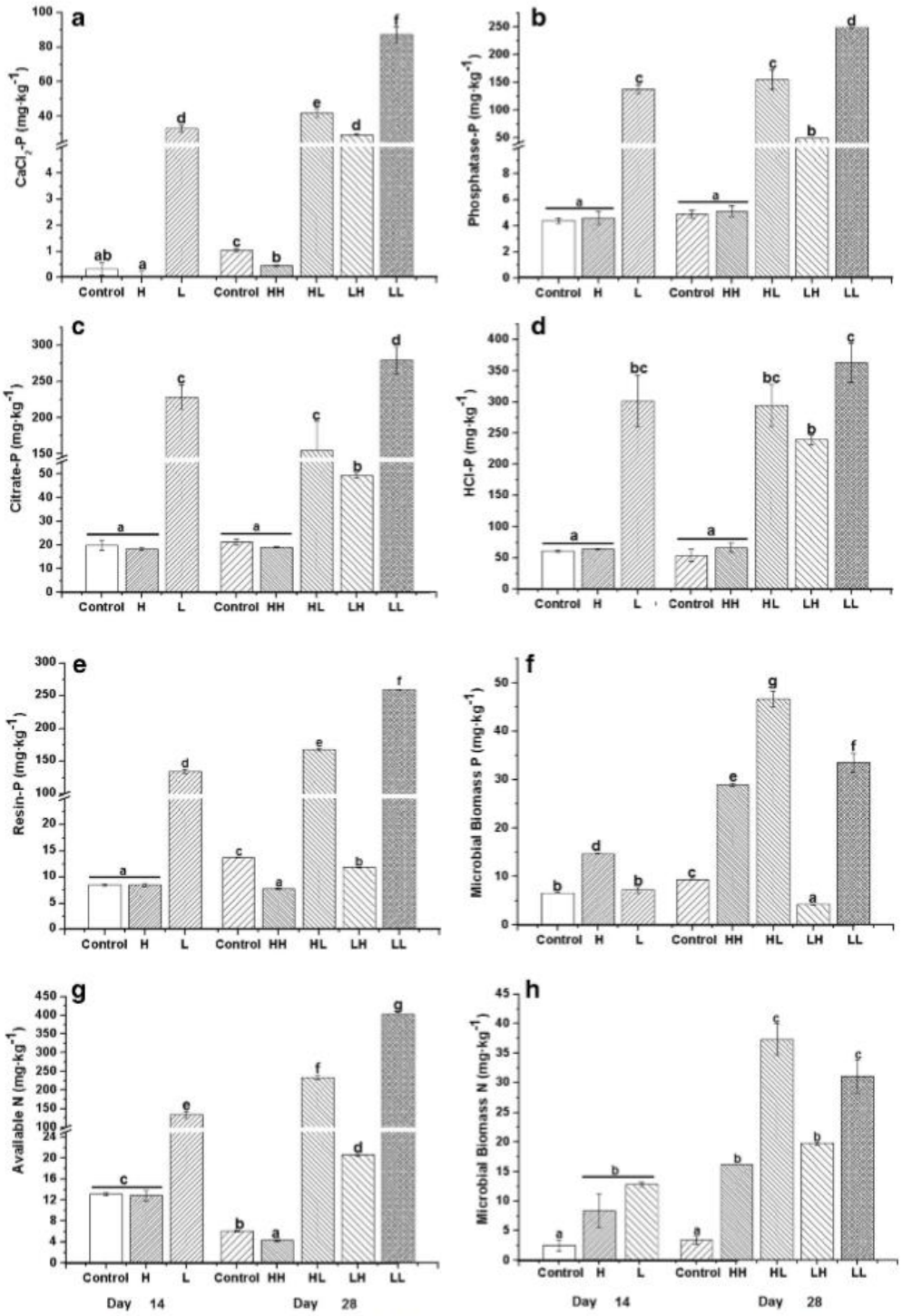

Fig 3 Experiment 1: $CaCl_2$-P (**a**), phosphatase-P (**b**), citrate-P (**c**), HCl-P (**d**), resin-P (**e**), microbial biomass P (**f**), available N (**g**) and microbial biomass N (**h**) (mg kg^{-1}) in detritusphere soils after the first (days 0 to 14) and the second (days 15 to 28) residue addition periods ($n = 4$). The soil was unamended (control) or amended with high (H) or low (L) C/P ratio residue on day 0 which was replaced on day 15 with H or L ($n = 4$). Different letters indicate significant differences between treatments based on log10-transformed data ($n = 4$; $P \leq 0.05$)

similar in L and H on day 14 and HH and LH on day 28. But MBN was about 3-fold higher in HL and LL than L or H.

Experiment 2

Two to 4-fold more P was bound to the AEM placed on faba bean detritusphere soil than in the control (Table 2). In week 1, more P was bound to the AEM on days 4 and 6 than on day 2. With faba bean, less P was bound to the AEM in week 2 than week 1, particularly on day 12 compared to day 6.

In the detritusphere of faba bean residue, P pools were 3- to 100-fold higher than the control (Fig. 4). Placement of AEM had no effect on P pools in the control. With faba bean, AEM placement compared to without AEM reduced $CaCl_2$ P by 40% and HCl-P by about 10% after 1 and 2 weeks. AEM placement had no effect on citrate P. AEM placement reduced phosphatase P compared to without AEM only in week 2 where it was 40% lower than without AEM.

Discussion

This study showed that within 2 weeks, P pools in the detritusphere were influenced by P supply and removal. The effect of the C/P ratio of the first residue added on P pools is in agreement with previous studies where residues were mixed into the soil (Dalal 1979; Alamgir and Marschner 2013a; Alamgir and Marschner 2013b; Hoang and Marschner 2017; Marschner et al. 2015). In contrast to these studies, the residue effect on the measured parameters in this study could only occur through the mesh. Further, the first residue was removed from the mesh before placing the second residue. Therefore in contrast to Marschner et al. (2015), residue particles of first and second residue had very little, if any, direct contact.

Residue switch (Experiment 1)

P pools and available N were higher in detritusphere of low C/P residue than that of high C/P residue and the control (Fig. 2). The higher P and N availability in the detritusphere of low C/P residue can be explained by its higher P and N concentration compared to barley (Alamgir and Marschner 2013a). The lower MBP and similar MBN compared to high C/P residue are likely due to rapid decomposition of the low C/P residue. This is corroborated by the larger amount of high C/P residue remaining after 2 weeks than of low C/P ratio. Residue weights are not available for this experiment, but in another experiment carried out under the same conditions and with the same initial residue amounts (3.6 g residue/microcosm), the residue amount after 2 weeks was 1.4 g for low C/P residue (60% reduction) and 3.0 g for high C/P residue (17% reduction). Therefore, by the end of 2 weeks, readily available C may have been depleted in low C/P residue resulting in microbial biomass turnover. In contrast, the high C/P residue decomposed more slowly and therefore supplied available C for longer.

The second addition of high C/P residue in HH had little effect on P pools compared to the single amendment in H. This is likely because these P pools were already low after the first H addition. MBP was higher in HH than H whereas MBN did not differ between HH and H. However, the increase in MBP in HH compared to H was small (about 3 mg kg^{-1}). This may have been too small to reduce resin P or the P pools through immobilisation. The lack of increase in MBN in HH compared to H together with the reduced available N indicates that microbial N uptake in HH was limited by N availability.

Most P pools (except HCl P), MBP, available N and MBN were higher with low C/P residue applied twice (LL) than only one addition (L) which can be explained by the release of nutrients (N, P and also C) during decomposition of the second L amendment. The lack of difference in HCl-P between L and LL could be due to the large size of the pool after the single L addition which may represent the maximum value of HCl P in this soil.

The first hypothesis (P pools will change depending on the order in which the residues are placed; when low C/P residue follows high C/P residue, measured parameters will be lower than with low C/P residue added twice. But when high C/P residue application follows low C/P residue, measured parameters will be higher than with high C/P residue added) can only be confirmed for some of the measured parameters. The hypothesis was based on Marschner et al. (2015) where residues were mixed into soil twice. Marschner et al. (2015) explained this "legacy effect" by decomposition of both previously added residue remaining in the soil and of the freshly added residue. In the present experiment, all measured parameters were higher on day 28 with low C/P following high C/P residue (HL) than with high C/P added twice (HH), which can

Table 2 P concentration of anion exchange membranes (three membrane strips/microcosm) in detritusphere of faba bean residue and the control

Residue	Week 1 (mg P/3 strips/microcosm)			Week 2 (mg P/3 strips/microcosm)		
	Day 2	Day 4	Day 6	Day 8	Day 10	Day 12
Faba bean	0.42*	0.68*	0.90*	0.36*	0.44*	0.27*
Control	0.12	0.14	0.27	0.19	0.15	0.05

*Significant differences between treatments, $p \leq 0.05$, $n = 4$

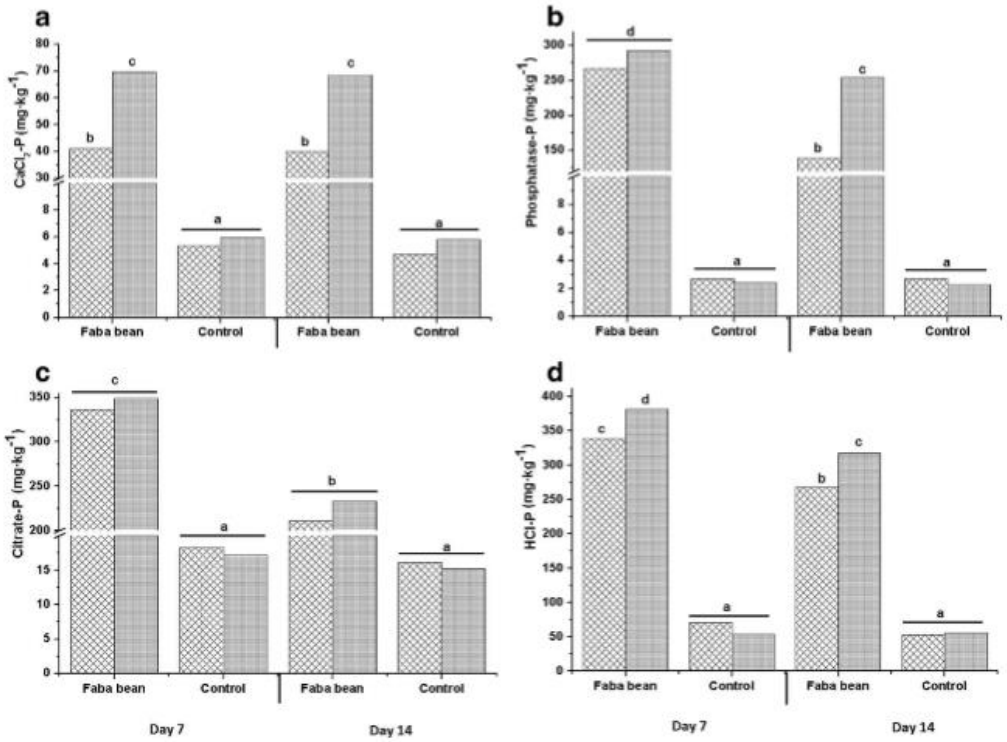

Fig. 4 Experiment 2: $CaCl_2$-P (**a**), phosphatase-P (**b**), citrate-P (**c**), HCl-P (**d**) (mg kg^{-1}) in control and faba bean detritusphere soils 7 and 14 days after removal of P with or without anion exchange membranes. Different letters indicate significant differences between treatments based on log10-transformed data ($n = 4$; $P \leq 0.05$)

be explained by the supply of easily available C, N and P by L added on day 14 in HL. Compared to low C/P residue added twice (LL), P pools (except HCl P) and available N were lower in HL. This legacy effect of the previously added H occurred although H remaining on the mesh was removed on day 14. Small particles of H may have fallen through the mesh in the first 14 days and may have also adhered to the mesh. This provided a longer-lasting C supply for microbes than in the low C/P residue alone and induced N and P immobilisation as evident in the higher MBP and MBN in HL compared to LL and also L on day 14. However, the amount of added low C/P residue in HL on day 14 was likely much larger than that of remaining high C/P residue. Thus, nutrient release from low C/P residue was greater than immobilisation and resulted in higher P pools and available N than H and HH.

With high C/P residue following low C/P residue (LH), P pools and available N were higher than with high C/P residue added twice (HH), but MBP was lower and MBN did not differ between the two treatments. Thus in LH, the remaining low C/P residue increased N and P availability compared to HH, but the amount of L left after addition of H likely limited C availability and thus microbial nutrient uptake compared to HH. However, compared to LL, all measured parameters were lower in LH. This can be explained by the low N and P concentration of the high C/P residue which would limit N and P release during decomposition after day 14 compared to LL.

In Marschner et al. (2015), available N and P were similar with low C/P following high C/P residue and with high C/P following low C/P residue. But in the present study, P pools (except HCl P), available N, MBP and MBN were lower in high C/P following low C/P residue (LH) than low C/P following high C/P residue (HL). This is likely because of the larger amount of second residue compared to the remaining first residue and the sampling in the detritusphere which would magnify the effect of the residue on the mesh. It should be noted that the results of the two studies may also be different due to the amount of P added with the residues. In the present study, 0.03 g P kg^{-1} and 0.18 g P kg^{-1} were added with high and low C/P residue whereas it was 0.002 g P kg^{-1} and 0.04 g P kg^{-1} with high and low C/P residue in Marschner et al. (2015). Thus, in this experiment compared to Marschner et al. (2015), the total amount of P added was greater and differences between H and L were smaller.

The results of this experiment demonstrate the dominating influence in the detritusphere of the residue added on day 14 due to the small amount of previous amendment left. It also

highlights the short-lived effect of surface-applied residues with different C/P ratio on soil nutrient availability after replacement with other residues. In the field, a similar situation may occur if harvest residues are eaten by animals, removed or wind and water off-site, followed by another application of organic materials.

Removal of P by AEM (Experiment 2)

The second hypothesis (the reduction in P pools induced by high C/P following low C/P residue can be mimicked by placement of anion exchange membranes on the detritusphere of low C/P residue) can be confirmed. Removal of P by AEM resulted in lower concentrations of most P pools in the faba bean detritusphere (Table 2, Fig. 4). A reduction of P pools in LH compared to L was also found in experiment 1.

The relative decrease was greatest in $CaCl_2$-P (by about 30%) which is considered to be the most available among the P pools measured by the DeLuca et al. (2015) method. However, phosphatase and HCl P were also reduced by AEM, confirming that they can be considered to be labile (DeLuca et al. 2015) and release P over a relatively short period of time (2 weeks) if available P is removed from the soil. The lack of effect of AEM on citrate P does not necessarily indicate that no P was removed from this pool. It is possible that P from this pool bound to the AEM was replenished by P released from other pools, e.g. HCl P.

Application of AEM in week 2 did not further decrease $CaCl_2$ P in faba bean detritusphere compared to week 1. This could indicate that the concentration reached by the end of week 1 was close to the equilibrium concentration relative to AEM. HCl P also did not further decrease suggesting that the remaining HCl P was less labile than that removed in week 1. However, AEM application further decreased phosphatase P and resin P indicating that these pools are depleted when supply of available P from $CaCl_2$ P and HCl P is low. The lack of effect in the control is likely due to the low P pool concentrations and consequently little P removal by AEM (Table 2). In contrast to experiment 2 where citrate P was not reduced by AEM, citrate P was about 5-fold lower in LH compared to L in experiment 1. The greater depletion of citrate P in LH may be due to release of organic acid anions during decomposition of H which depleted citrate P (Iyamuremye et al. 1996). In contrast, P removal by AEM would only involve reduction of soil solution P and release of bound P to replenish it.

Conclusion

This study showed that P pools in the detritusphere are influenced within 2weeks by P supply and removal and that a change in C/P ratio of the applied residue resulted in either decrease or increase in soil P pools. For the field situation, this suggests that the effect on soil P pools of a given residue mulch rapidly disappears after replacement with another mulch as it may occur when harvest residues are removed and organic amendments are applied. Further studies could track residue P by using ^{33}P-labelled residues.

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Chapter 6. Wheat growth induced changes in P pools in the detritusphere of crop residues.

Wheat growth-induced changes in phosphorus pools in the detritusphere of crop residues with different C/nutrient ratio.

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Conribution to the Paper	Performed experiment, analysed soil samples, analysed and interpreted data and wrote the manuscript		
Overall percentage (%)	**70%**		
Certification	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligation or contractual agreements with a thrid party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate to include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Wheat growth-induced changes in phosphorus pools in the detritusphere of crop residues with different C/nutrient ratio

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Abstract

In the field, roots often grow around decomposing crop residues creating a rhizosphere/detritusphere interface. P pools and N availability in the rhizosphere and detritusphere have been extensively studied, but separately. However, little is known about P pools and N availability in the rhizosphere/detritusphere interface. An experiment was carried out to determine the influence of residue C/nutrient ratio on P pools and N availability in wheat rhizosphere. Two crop residues, low C/nutrient faba bean residue and high C/nutrient barley straw were used. The experimental microcosms included an upper and a lower PVC core. The bottom end of the upper core and both ends of the lower core were covered by nylon mesh. To the lower core, crop residues were added as a thin uniform layer on the top mesh. The bottom end of the upper core and top end of the lower core were joined and held in place by tape so that the residues were sandwiched between the two cores. Wheat was planted in the upper core of half of the microcosms. Treatments used in the experiment were control without residue or wheat growth, wheat growth without crop residue, barley straw without or with wheat growth, barley, faba bean residue without or with wheat growth. After 14 and 28 days of wheat growth, dry weights of remaining crop residues and of wheat plants, P concentration and P uptake by plants were measured. Bioavailable P pools [anion exchange (resin) P; P bound to soil particles: citrate and HCl P; and microbial P), available N and microbial biomass N were measured in wheat rhizosphere alone, detritusphere of faba bean residue and barley straw, and in the rhizosphere/detritusphere interface. Faba bean residue mass loss was greater than that of straw; and mass loss was greater in the detritusphere alone than in the rhizosphere/detritusphere interface. Plant P concentration and P uptake were higher with faba bean than with straw and unamended wheat plants. With faba bean, P pools and N availability, but not MBP and MBN, were lower in the rhizosphere/detritusphere interface than detritusphere alone, likely due to plant uptake. P pools were higher in detritusphere of faba bean residue than wheat rhizosphere alone. With straw, P pools and MBN were low and not affected by wheat roots. MBP was higher in the rhizosphere/detritusphere interface than the detritusphere. This study showed that presence of roots reduced residue decomposition. P pools and N availability in the rhizosphere/detritusphere interface were influenced by residue type, and plant nutrient uptake reduced P pools and available N only with low C/nutrient residue.

Keywords: C/nutrient ratio, detritusphere, P pools, rhizosphere, wheat

1. Introduction

The rhizosphere and detritusphere are two of the three hotspots of microbial activity in the soil (Ge et al., 2017; Kuzyakov and Blagodatskaya, 2015). The rhizosphere is the soil within approximately 2 mm distance from the root surface (Dotaniya and Meena, 2015; Hiltner, 1904). The rhizosphere is characterised by high concentrations of easily available compounds that are released from plant roots (Mendes et al., 2013), compared to the bulk soil. The rhizosphere also supports a larger and more active microbial biomass than the bulk soil (Hoyle et al., 2008). Low molecular weight organic compounds, for example, organic acid anions, released by plant roots compete with phosphorus (P) sorbed onto metal oxides (Bolan et al., 1994; Hinsinger, 2001), resulting in the release of P into soil solution for plant (and microbial) uptake. Nutrients released by exudates or microbes can be taken up by plant roots or immobilized into the microbial biomass, leading to the formation of a nutrient depletion zone around the roots (Darrah, 1993).

The detritusphere is defined as the soil within approximately ≤ 5 mm distance from decomposing residues (Liu et al., 2011). Compared to the bulk soil, the detritusphere is characterised by a higher concentration of easily available compounds, especially in the early stages of residue decomposition (Poll et al., 2010). Microbial decomposition of crop residues can provide an important source of nutrients for plants and soil organisms (Noack et al., 2012). The C/nutrient ratio of the crop residue influences nutrient release and microbial activity in the detritusphere (Abiven et al., 2005; Jensen et al., 2005). For example, crop residues with C/N > 25 and C/P > 200 are decomposed slowly and induce temporary net nutrient immobilisation in the microbial biomass (Alamgir et al., 2012; Chen et al., 2014; Trinsoutrot et al., 2000). In contrast, addition of crop residues with low C/nutrient ratio (C/N < 20; C/P 89) leads to net nutrient release (Nguyen and Marschner, 2017). Recently, Erinle et al. (2018) showed that compared to the unamended control, available P and labile P pools were several fold higher in the detritusphere of low C/P residue (C/P 38), but unchanged in the detritusphere of high C/P residue (C/P 255).

In the field, roots often grow around decomposing crop residues where rhizosphere and detritusphere may interact to create an interface that is influenced by both rhizosphere and detritusphere properties (Marschner et al., 2012). The mechanisms by which crop residue decomposition influences the rhizosphere have been reviewed by Dormaar (1990) and Cheng and Kuzyakov (2005). Residue decomposition may be increased in the rhizosphere due to higher microbial activity (Jiao et al., 2019; Wei et al., 2019). This has been termed rhizosphere priming effect (Huo et al., 2017; Liu et al., 2017). Faster rates of residue decomposition have been linked to higher microbial functional diversity and microbial enzyme activity (Acosta-

Martinez et al., 2014; McDaniel et al., 2014). However, most of these studies have not studied nutrient availability in the rhizosphere/detritusphere interface.

The aim of the experiment was to determine the effect of plant roots and crop residues in the soil adjacent to the roots (rhizosphere), to residues (detritusphere) and the rhizosphere/detritusphere interface on P pools and N availability. We hypothesised that (1) with low C/nutrient organic material, P pools and nutrient availability will be lower in the rhizosphere/detritusphere interface than detritusphere due to plant uptake, but higher than in the rhizosphere due to net nutrient release from the organic material, and (2) with high C/nutrient organic material, P pools and nutrient availability will be lower in the detritusphere/rhizosphere interface than the rhizosphere or detritusphere.

2. Materials and methods

2.1 Soil and plant residues

As described in Erinle et al. (2018), 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 for over 80 years. This area has a Mediterranean climate. The soil is a Chromosol in Australian soil classification, and a Rhodoxeralf in US Soil Taxonomy. The soil was dried at 40°C and sieved to < 2 mm. The properties of the soil are as follows: pH 6.8 (1:5 soil/water); clay 25%; sand 37%; silt 37%; EC (1:5) 0.1 dS m^{-1}, total organic C 17 g kg^{-1}, total organic N 1.5 g kg^{-1}, total P 302 mg kg^{-1}; bulk density 1.3 g cm^{-3}, maximum water-holding capacity (WHC) 349 g kg^{-1}.

The two types of crop residues used were young faba bean shoot (*Vicia faba* L.) as low C/P residue, and mature barley straw (*Hordeum vulgare* L.) as high C/P residue, referred to as faba bean (F) and straw (S). The residues were dried at 40°C in a fan-forced oven, ground and sieved to 0.25–2 mm particle size. Total P was about four-fold higher in young faba bean shoots than mature barley straw (Table 1).

2.2 Experimental design

The experimental microcosms comprised of two PVC cores, an upper core (5 cm height × 3.5 cm diameter) and a lower core (2.5 cm height × 3.5 cm diameter) (Fig. 1). The bottom end of both cores was covered by a nylon mesh (mesh size 0.1 mm × 0.8 mm). The cores were filled with soil (in g dry soil equivalent): upper core 50 g and lower core 25 g, Reverse osmosis (RO) water was added to achieve 50% maximum WHC. The soil was maintained at this water content for one week. Then the top of the lower core was covered by mesh and crop residues were added (20 g·kg^{-1}) as a thin uniform layer. The bottom end of the upper and top end of the lower core were joined with the residue sandwiched between the cores. The cores were held in place

by tape. Then, five pre-germinated wheat seedlings (*Triticum aestivum* L., variety Axe) were planted into the upper core. After five days, the plants were thinned to three seedlings per core. The plants were grown for 14 or 28 days. There were six treatments with four replicates per treatment and sampling time: control without residue or wheat growth (Co), without residue but with wheat growth (Wheat), barley straw without wheat (S), barley straw with wheat growth (S+W), faba bean residue without wheat (F), and faba bean residue with wheat growth (F+W). The cores were then exposed to natural light at 20-25 °C for 14 or 28 days. Soil water content was checked daily by weight and water was added if necessary.

2.3 Sampling

Four replicates of each treatment were harvested after 14 and 28 days of planting for soil and plant analyses. After 14 days, roots had formed a layer on the mesh separating the roots from the residues, some roots had penetrated the mesh and grew into the underlying residues. To collect soil samples, the tape was removed and the cores carefully separated. For treatments with plant alone, soil in the 0-2 mm layer on top of the mesh (in the upper core) was sampled for rhizosphere soil. For treatments with residue alone, soil in both upper and lower PVC cores in 0-2 mm from the mesh was sampled for detritusphere soil. For treatments with plant and residue, soil in the 0-2 mm layer on top of the mesh (in the upper core), which included rhizosphere and detritusphere was sampled for rhizosphere/detritusphere.

Plant dry weight was determined after drying at 50 °C for 48 h. Shoots and roots were combined to have sufficient dry matter for analysis.

2.4 Analyses

Measurements were carried out as described in Erinle et al. (2018). Briefly, soil maximum water holding capacity was measured at matric potential -10kPa (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 (Rayment and Higginson, 1992). Total organic C of soil and residues was determined by wet oxidation (Walkley and Black, 1934). Soil total N content was determined by a modified Kjeldahl method (Vanlauwe et al., 1996). Total P in the soil was determined by the phospho-vanado molybdate method (Hanson 1950) after acid digestion with HNO_3-HClO at a 4:1 ratio. Total P of wheat plant and crop residues (faba bean residue and barley straw) was digested with HNO_3 and H_2O_2 at a 4:1 ratio and determined by the same as total soil P. Total N in soil and plant residues was determined using the Kjeldahl method (McKenzie and Wallace, 1954). Water-soluble P in the residues was extracted with hot water modified after Konieczynski and Wesolowski (2007). To 1 g residue, 30 mL of hot (85 °C) RO water was added, then shaken for 2 h and filtered. The filtrate P concentration was

measured colorimetrically (630 nm) using the malachite-green method (Ohno and Zibilske, 1991). Water extractable carbon was determined following similar procedure, but with 0.25 g residue. Organic C in the filtrate was determined by the Walkley and Black method (Walkley and Black, 1934).

Soil P pools were measured using a modification of DeLuca et al. (2015). Two pools of the DeLuca method were not measured. $CaCl_2$ P (representing the soluble and weakly adsorbed inorganic P) was replaced by anion extractable (resin) P, both are available P pools. Phosphatase labile organic P was not measured because we found in earlier studies, that the phosphatase P concentration in this soil was very low and variable. Microbial biomass P was measured because it is a potentially available P pool from which P is released upon biomass turnover. Citrate P and HCl P were extracted in parallel by shaking 0.5 g of soil with 10 ml of either 10 mM citric acid or 1 M HCl in separate 50 mL tubes for 3 h on an end-over-end shaker. P pools extracted are active inorganic P sorbed to clay particles (citrate P) or weakly bound in inorganic precipitates (HCl P). Resin (available) P and microbial biomass P (MBP) were determined with the anion exchange resin method (Kouno et al., 1995), with hexanol as fumigant. The P concentration in the extracts was determined colorimetrically (630 nm) using the malachite-green method (Ohno and Zibilske, 1991). MBP is the difference in P concentration between fumigated and un-fumigated soil (Kouno et al., 1995). Available N (ammonium and nitrate) concentration was measured 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 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 (Moore et al., 2000).

2.5 Statistical analysis

To achieve normal distribution, data of microbial biomass, N and P availability and P pools were was log10 transformed and then analysed by one-way repeated measures ANOVA with between subjects factor-treatment, within subjects factor-time in SPSS statistics version 25. Tukey's multiple comparison test at 95% confidence interval was used to determine significant differences among treatments at a given sampling time and for a treatment between sampling times.

3. Results

Residue dry weight on days 14 and 28 was greater with straw than faba bean and greater with plants than without (Table 2). Compared to the initial value (1.5 g), straw weight was 40%

lower without plants and 20% lower with plants; weight of faba bean was 70% and 60% lower without plants and with plants, respectively. On day 28, residue weight was about 10% lower than on day 14 except in faba bean with plants where it did not change.

Wheat plant dry weight was not affected by residue presence (Table 3). It increased by 20-70% from day 14 to 28 with the smallest increase in wheat alone. Wheat P concentration on day 14 was greater with residues than wheat alone (Table 3). Compared to wheat alone, the P concentration was 30% higher with straw and 50% higher with faba bean. P concentration decreased by 30% from day 14 to 28 with straw, changed little in wheat alone and with faba bean. On day 28, the P concentration was 50% higher with faba bean than wheat alone and with straw. At both sampling times, wheat P uptake did not differ between wheat alone and with straw, but it was about two-fold higher with faba bean than wheat alone. P uptake changed little from day 14 to 28.

Citrate P, HCl P and resin P were higher with faba bean than the control, wheat alone and with straw, which did not differ (Fig. 2). Presence of plants influenced these P pools only with faba bean where they were lower with than without wheat. Citrate P with faba bean on day 14 was about 10-fold higher that in the control and about 10% lower with wheat than without (Fig. 2a). From day 14 to 28, citrate P remained unchanged in the control, wheat alone and with straw alone, but decreased by 50% in straw with wheat and three to five-fold with faba bean. On day 28, citrate P with faba bean was two to three-fold higher than the control and 50% lower with wheat than without.

On day 14, HCl P with faba bean was about two-fold higher than the control, and was 10% lower with wheat than faba bean alone (Fig, 3b). HCl P increased by 15% from day 14 to 28 in the control but in faba bean with wheat it was 30% lower on day 28. On day 28, HCl P was two-fold higher in faba bean alone than the control, but did not differ between control and faba bean with wheat.

On both sampling days, resin P in faba bean alone was four to five-fold higher than the control, but only two to three-fold higher in faba bean with wheat (Fig, 3c). With faba bean, presence of plants reduced resin P, by 30% on day 14 and by 50% on day 28. Compared to day 14, resin P on day 28 was about 20 to 30% lower in wheat alone, straw alone and barley with wheat and with faba bean alone, but two-fold lower with faba bean with wheat.

MBP on day 14 was lowest in faba bean alone and highest in straw with wheat (Fig. 3d). MBP did not differ between control, wheat alone, straw alone and faba bean with wheat. In both straw and faba bean, wheat growth increased MBP compared to residues alone, by 20% in straw and

two-fold in faba bean. MBP on day 28 was 20 to 60% higher than on day 14. On day 28, MBP did not differ between control, wheat alone and faba bean alone. Compared to the control, it was about 30% higher in straw alone, 70% higher in straw with wheat and two-fold higher in faba bean with wheat.

On day 14, available N was lowest in straw with wheat and highest in faba bean alone. In residue treatments, available N was lower with wheat than without. Compared to the control, available N was about 70% lower in wheat alone, 50% lower in straw alone, 80% lower in straw with wheat. But it was about two-fold higher in faba bean treatments, with a greater increase without plants than with wheat. Available N on day 28 was about 50% lower than on day 14 in most treatments except in straw with wheat where it remained unchanged. On day 28, available N was 80% lower than the control in wheat alone and straw treatments. But it was three-fold higher in faba bean alone and two-fold higher in faba bean with wheat.

MBN on day 14 did not differ between control, wheat alone and straw with wheat. Compared to the control, MBN was 50% lower in straw alone, two-fold higher in faba bean alone and more than three-fold higher in faba bean with wheat. From day 14 to 28, MBN decreased by about 50% in control and wheat alone, but it increased two-fold in straw alone and by about 30% with faba bean. On day 28, MBN did not differ between control, wheat alone and straw treatments. Compared to the control, MBN was 10-fold higher in faba bean alone and 15-fold higher in faba bean with wheat.

4. Discussion

Based on the results of this experiment, the first hypothesis (with low C/nutrient organic material, P pools and nutrient availability will be lower in the rhizosphere/detritusphere interface than detritusphere due to plant uptake, but higher than in the rhizosphere) can be confirmed for most P pools and available N, but not for MBP and MBN. The second hypothesis (with high C/nutrient organic material, P pools and nutrient availability will be lower in the detritusphere/rhizosphere interface than the rhizosphere or detritusphere) has to be declined except for available N on day 14.

The greater residue dry weight with plants than without plants could be due to presence of roots that grew through the nylon mesh into the residue layer, which may have led to underestimation of residue weight loss. This can also be explained by the release of root exudates which include a large proportion of low molecular weight and water soluble compounds (Gang et al., 2012; Gargallo-Garriga et al., 2018). These compounds are more easily decomposable than residues that contain a large proportion of high molecular-weight structural carbohydrates. Microbes are likely to preferentially use low molecular weight exudates and be less reliant on residues as

energy source. Improved organic C availability to microbes thus microbial growth in the interface is corroborated by the higher microbial biomass P and N in the detritusphere/rhizosphere interface than in the detritusphere.

Faba bean residue decomposed more quickly than barley straw, which can be explained by its low C/nutrient ratio (Abiven et al., 2005; Jensen et al., 2005). Decomposing faba bean residue released large amounts of P which not only increased wheat P uptake but also P pools compared to wheat alone and barley with wheat, which is in agreement with our earlier study (Erinle et al., 2018). Presence of wheat roots reduced resin P, citrate P and HCl P compared to faba bean alone. This can be explained by P uptake by plants and microbes. The reduction of citrate P and HCl P could also be the release of organic acid anions from roots and decomposing faba bean residues that exchanged P from soil minerals (Fink et al., 2016; Nziguheba et al., 2000) and thereby reduced citrate and HCl labile P. The mobilised P may have been taken up by the plants or converted into pools not assessed by the Deluca method. The lower available N in faba bean with plants than without can be explained by plant N uptake, but also by microbial N uptake because MBN was higher with plants than without.

Due to the low nutrient release from barley, citrate P, HCl P and resin P did not differ from the control. These P pools were apparently so low that they could not be further decreased by the growing wheat plants. However, MBP was higher than the control and wheat alone. This suggests that barley decomposition released P either from the residue itself, through priming of native soil organic matter (Almeida et al., 2018; Dijkstra et al., 2013) or from soil particles by ligand exchange with organic acid anions (Fink et al., 2016; Nziguheba et al., 2000). Resin P, on the other hand, did not differ between control and barley treatments. The lack of net immobilisation with P can be explained by the P buffering capacity of the soil (Holford and Crocker, 1991; Holford, 1976). MBN did not differ between barley and the control whereas available N was lower in barley treatments than the control. Thus, the lower available N with barley cannot be explained by higher microbial N uptake. In barley with wheat, the plants may have taken up N. Another reason for the lower available N with barley may be denitrification due to the higher microbial activity in barley treatments than the control. Oxygen depletion by high respiration rates can result in anaerobic microsites and therefore enhance denitrification (Schlüter et al., 2018). This would have also occurred in the faba bean treatments, but was masked by the high N released from faba bean residues.

Conclusion

This study showed that presence of roots reduced residue decomposition. Nevertheless, decomposition of low C/P residue released sufficient P to enhance plant P uptake and P pools

as well as available N compared to the unamended soil and that amended with barley. Studies with ^{33}P labelled residues could be used to understand the fate of residue P and to evaluate the role of native soil P in the plant-soil system.

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Table 1. Total organic C, N, P, water-extractable P, C/N ratio, C/P ratio of high C/P (mature Straw straw) and low C/P (young faba bean shoot) and residues (n = 4). Different letters indicate significant differences between residues ($P < 0.05$, from Erinle et al., 2018).

Properties	**High C/P**	**Low C/P**
Total organic C (g kg^{-1})	408 b	347 a
Total N (g kg^{-1})	4.3 a	38.5 b
Total P (g kg^{-1})	1.7 a	9.2 b
Water extractable P (g kg^{-1})	0.1 a	6.5 b
Water extractable organic C (g kg^{-1})	20 a	420 b
C/P ratio	255 b	38 a
C/N ratio	95 b	9 a

Table 2. Residue dry weight in detritusphere of mature barley straw and young faba bean shoot without (barley straw and Faba bean) and with wheat growth after 14 and 28 days incubation (initial weight = 1.5 g). Different letters indicate significant differences among treatments ($P < 0.05$) for each sampling time.

Treatment	Residue dry weight (g)	
	Day 14	Day 28
Straw	0.88 c*	0.74 c
Straw+Wheat	1.24 d*	1.15 d
Faba bean	0.45 a*	0.41 a
Faba bean+Wheat	0.57 b	0.58 b

Table 3. Plant dry weight (g core^{-1}), P concentration (mg g^{-1}) and P uptake (mg core^{-1}) in planted treatments without residue (Wheat) or with barley straw or faba bean residue (Straw+Wheat or Faba bean+Wheat) after plant growth for 14 and 28 days. Different letters indicate significant differences among treatments ($P < 0.05$) at a given sampling time and an asterisk indicates significantly higher values in a treatment between sampling times.

Treatment	Plant dry weight (g core^{-1})		P concentration (mg g^{-1})		P uptake (mg core^{-1})	
	Day 14	Day 28	Day 14	Day 28	Day 14	Day 28
Wheat	0.11 a	0.13 a*	4.78 a	4.50 a	0.51 a	0.61 a*
Straw+Wheat	0.10 a	0.17 a*	6.44 b*	4.51 a	0.67 ab	0.77 a
Faba bean+Wheat	0.11 a	0.18 a*	8.00 c	8.38 b	0.91 b	1.52 b

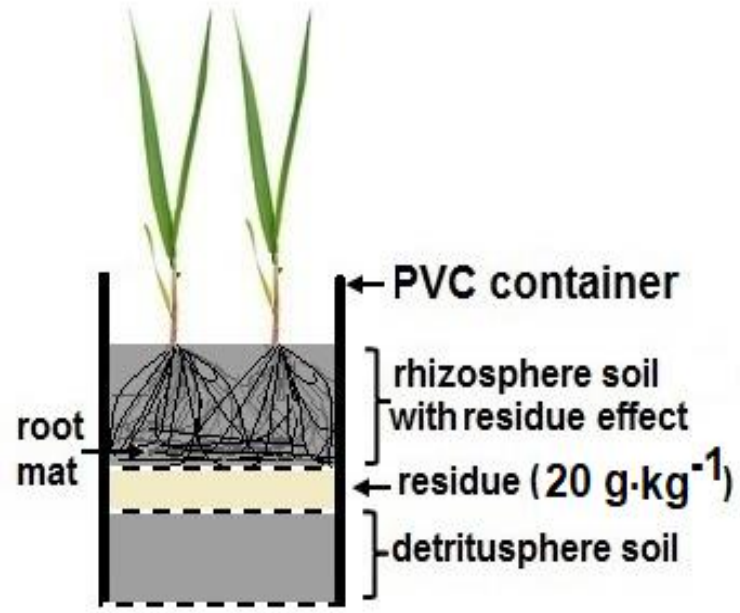

Fig. 1. Schematic diagram of microcosms used in the study. The dotted lines indicate mesh layers.

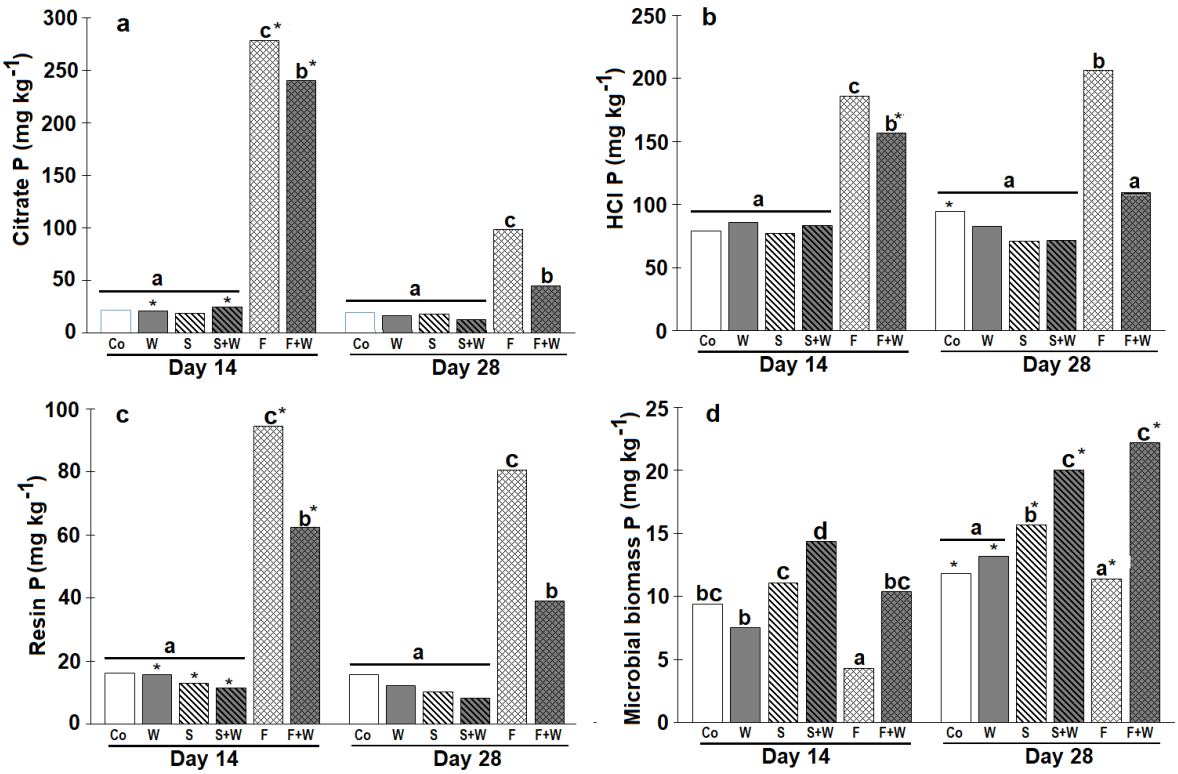

Fig. 2. Citrate P (a), HCl P (b), resin P (c) and microbial biomass P (d) in the control without plants or residues (Co), rhizosphere of wheat plant alone (Wheat), and in the detritusphere of straw and young faba bean shoot alone (S and F) and with wheat growth (S+W and F+W) after 14 and 28 days (n= 4). Different letters indicate significant differences ($P < 0.05$) between treatments at a given sampling time and an asterisk indicates significantly higher values in a treatment between sampling times based on log10-transformed data.

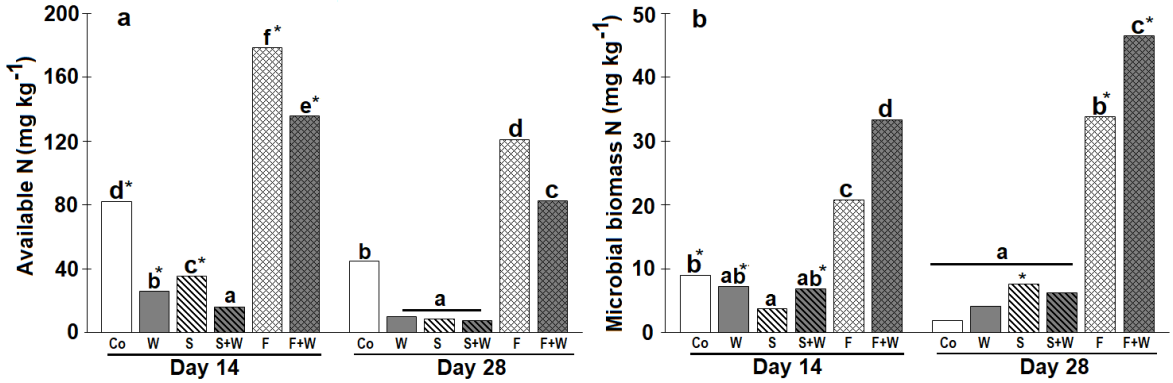

Fig. 3. Available N (a) and microbial biomass N (b) in the control without plants or residues, (Co) rhizosphere of wheat plant alone (Wheat), and in the detritusphere of mature barley straw and young faba bean shoot without (S and F) and with wheat growth (S+W and F+W) after 14 and 28 days (n = 4). Different letters indicate significant differences ($P < 0.05$) between treatments at a given sampling time and an asterisk indicates significantly higher value in a treatment between sampling times based on log10-transformed data.

Chapter 7. Conclusions and Future Research

Phosphorus (P) deficiency as a result of rapid conversion of available P to less available pools and low soil solution P (Frossard et al., 2000; Randriamanantsoa et al., 2015) is one of the largest constraints to food production. Inorganic fertilizers supply P in forms readily available for plant uptake, but more than 80% of the applied P can become immobile and unavailable for plant uptake (Schachtman et al., 1998). On the other hand, the incorporation of crop residues into the soil can improve soil health by increasing microbial functions and also return nutrients to the soil. However, the amount of P released depends on the chemical composition (such as C/P ratio) of the added crop residue. For example, high P residues (>5 mg P kg^{-1}, C:P <200) are rapidly decomposed and induce net P mineralisation whereas low P residues (<5 mg P kg^{-1}, C:P >200) decompose slowly and can cause net P immobilisation (Tian et al., 1992; Brady and Weil, 2002; Mat-Hassan, 2012).

The effects of crop residue mixed into soil on nutrient availability has been extensively studied. But residues may also form a layer on the soil surface, for example in no-till farming systems, where nutrients mineralised during residue decomposition are released into the adjacent soil within about ≤ 5 mm from the decomposing residue. This soil zone is called the detritusphere (Gaillard et al., 2003; Liu et al., 2011). The detritusphere is characterised by high concentrations of mineral nutrients and organic compounds (Petersen et al., 1993; Ball, 2001; de Neergaard and Magid, 2015).

P pools in the detritusphere of decomposing crop residues have not been well studied. Also, little is known about the effect of other factors such as soil water availability and plant roots on P pools in detritusphere of crop residues differing in C/P ratios. Hence, experiments described in this thesis were designed to address these knowledge gaps. The results are summarised around three major factors that were studied in this project (Fig. 7.1).

(a) In order to investigate the *influence of soil water availability* on P pools in the detritusphere, experiments with drying and rewetting and constant soil water content were carried out using crop residues with contrasting C/P ratios. In Chapter 2, the influence of drying and rewetting on soil P pools in the detritusphere of young faba bean (C/P 38) and mature barley straw (C/P 255) was studied. As expected from previous studies, rewetting of dry soils induced a respiration flush and the flush was greater with faba bean than barley. The higher P pools in faba bean detritusphere than in barley can be explained by the lower C/P ratio of the former. In general, drying and rewetting had little effect on P pools. However, the experiment where anion exchange resins were placed into the soil before rewetting showed that in faba bean

detritusphere, P was released upon rewetting. Removal of P by the AEM induced a reduction of P pools compared to rewet soil without anion exchange resins. The lack of effect on P pools in the first experiment suggests that P released upon rewetting is rapidly adsorbed to soil particles if not removed from the soil solution by AEM.

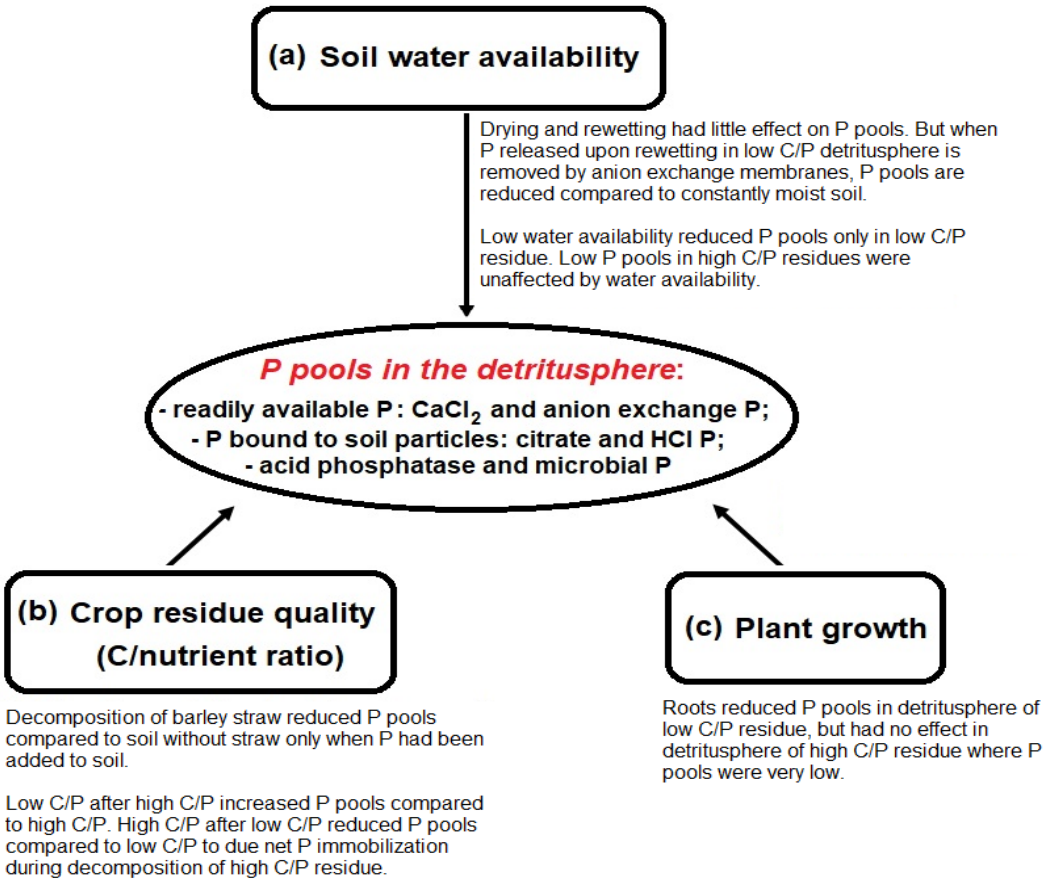

Fig. 7.1. Schematic diagram summarizing the effect of soil water availability, crop residue quality (C/nutrient ratio) and plant growth on P pools in the detritusphere.

Drying and rewetting are drastic changes in soil water availability. Regarding the effect of water availability on P pools in the detritusphere, periods moderate changes in water availability should also be considered. The experiment described in Chapter 3 mimicked situations where soil under residues is first moist, but then dries. In the detritusphere of the residue mix, where P pools and respiration were high at high water availability, low water availability strongly reduced P pools and respiration. This shows that when nutrient-rich residues are decomposed, the limited diffusion of water and nutrients due to low soil water content can strongly reduce P pools. In the barley detritusphere on the other hand, low water content had little effect because microbial activity is limited by nutrient availability even at sufficient water availability.

(b)The experiments in Chapters 4 and 5 investigated the *influence of crop residue quality* on P pools in the detritusphere. In Chapter 4, inorganic N and P were added to the soil before it was

amended with mature barley straw with low decomposability (C/P 255) to generate detritusphere. Addition of inorganic N to soil increased P pools likely due to enhanced mineralisation of native soil organic matter. However, addition of N reduced straw decomposition, suggesting that N addition reduced straw mass loss via respiration. Barley straw decomposition reduced available P pools in the detritusphere, particularly in soil to which inorganic P was added. This indicates that the effect of high C/P residues on P pools will be more pronounced in fertilised soil.

The aim of the experiments described in Chapter 5 was to assess the influence of residue switch on P pools in the detritusphere of crop residues with differing C/P ratios. After two weeks of incubation with young faba bean residue (L) or mature barley straw (H), the residues were replaced with either a H or L, resulting in four residue treatments: high-high (HH), high-low (HL), low-low (LL) or low-high (LH), which were incubated for another 14 days. In agreement with the previous experiments, P pools and available N on day 14 were higher, but MBP and MBN were lower in L than in H. On day 28, P pools and available N followed the order LL>HL>LH>HH, whereas MBN and MBP were highest in HL. The lower P pools in LH compared to LL can be explained by P immobilisation by microbes decomposing H. The finding that P pools on day 28 were higher in HL than LH suggests that the second residue added has a stronger influence on P pools than the initial residue, likely because of the greater amount of the second residue. This study showed that a change in the C/P ratio of added residue can either decrease or increase concentrations of various soil P pools. Following from this, another experiment was carried out to determine if the reduction of P pools after replacement of low C/P residue by high C/P residue in the residue switch experiment could be mimicked by using anion exchange membranes as P sink. Detritusphere soil was generated using faba bean residue. After two weeks moist incubation, the residues were removed and either replaced with AEM strips or left without AEM. Removal of P by AEM decreased most P pools in faba bean detritusphere, which is in agreement with the lower P pools in LH on day 28 than L on day 14.

(c) The aim of the experiment described in Chapter 6 was to assess the *influence of wheat growth* on P pools in the detritusphere. Pre-germinated wheat seeds were sown in unamended soil or soil amended with two crop residues of contrasting C/P ratios (young faba bean residue, C/P 38; mature barley straw, C/P 255). After 28 days with faba bean, P uptake in wheat was higher than with barley straw and control. P pools were lower in the interface of wheat rhizosphere and faba bean detritusphere than in detritusphere alone, due to plant uptake. With barley straw, presence of wheat roots had no effect on P pools. These results indicate that the effect of plants on P pools in the rhizosphere/detritusphere interface were influenced by residue type. Nutrients released during decomposition of low C/P residues were taken up by wheat which reduced P

pools and available N in the rhizosphere/detritusphere interface. In contrast, P pools in barley straw detritusphere were too low to be further reduced by roots.

Suggestions for future studies

The experiments described in this thesis answered a number of questions with respect to the effect of soil water availability, crop residue quality and wheat growth on P pools in detritusphere of crop residues differing in C/P ratios. However, there are research gaps arising from this study that could be addressed in future studies:

1. In all experiments, the detritusphere soil was collected in about ≤ 2 mm distance from the residues to maximise the detritusphere effect. To assess the extent of the detritusphere and how it is affected by soil water content and residue properties, future experiments could analyse soil in different distances from the residues.
2. In Mediterranean climates, soils are frequently exposed to drying and rewetting; fluctuations in soil water content can affect the rate of crop residue decomposition and P chemistry. In Australia, the fallow period between harvest of legumes and sowing of cereals can be up to 7 months; during this time drying and rewetting cycles may occur. Therefore, it is necessary to assess the effect of more than one drying and rewetting event on P release from crop residues and P pools in the soil. Also, P released at rewetting was removed by the AEM, inducing a reduction of P pools compared to rewet soil without anion exchange resins. The experiment with wheat plants showed that plants can reduce P pools in the detritusphere of low C/P residue. But the role of plants on P pools after rewetting of dry soil is unclear. Therefore, future experiments could test the effect of plant growth on changes in P pools in the detritusphere with repeated drying-rewetting events.
3. In the field, particularly in regions with limited access to water for crop production, there is the need to achieve a balance between water supply, nutrient addition and crop yield. In the experiment described in Chapter 3, detritusphere was generated at sufficient water supply. After removal of the residues, the soil was dried to different water contents. To mimic field conditions, residue decomposition should be carried out at different water contents either by placing the residues on soil with different water content or by varying the water content of the residues. Such experiments could also include plants.

4. The experiment described in Chapter 4 could not assess the source of P in the P pools. The experiment could be repeated with ^{33}P labelled fertiliser. With this approach, P movement from soil into residues could also be assessed. Use of ^{15}N labelled fertiliser would allow tracking the fate of fertiliser N in available N, microbial N and residues. If this experiment included plants, the effect of residues on fertiliser N and P uptake by plants could be studied.

5. The method used in this study for P pools does not provide detailed molecular and structural characterisation of P. A detailed speciation of P in soil and crop residues by ^{31}P nuclear magnetic resonance spectroscopy or X-ray absorption spectroscopy could increase the understanding of soil P pools. In all experiments, the relative contribution of P released from crop residues and native soil P to changes in P pools could not be quantified. To distinguish native soil P and added P, studies with ^{32}P labelled residue or fertiliser would be necessary.

6. Soil microbial communities are drivers of crop residue decomposition. However, in the studies described in this thesis, the effects of crop residue on microbial community composition or gene abundance was not determined. Therefore, future experiments could focus on investigating microbial community composition or gene abundance in residues and detritusphere soil during decomposition under different soil water availabilities, dry-rewetting conditions and residue switches.

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