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Effect of soil phosphorus availability and residue quality on phosphorus transfer from crop residues to the following wheat

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Abstract

Background and aims Legume break crops provide a series of agronomic benefits to the following wheat crop in a rotation. Phosphorus-efficient break-crop plants can mobilise P from non-labile pools in the soil and this could be made available to wheat plants after the decomposition of the break-crop residues. This study aimed to examine the contribution to P uptake by wheat plants, of residues from five different break crops with different maturities and C:P ratios.
Methods The wheat plants were grown in a soil that varied in P status (Olsen P 7 to 30 mg kg^{-1}) and was labelled with ^{32}P and amended with crop residues at a rate of 1% (w/w). Soil and plant samples were taken after 42 days of plant growth. Wheat plants were analysed for growth and P uptake. Soil samples were analysed for P availability and microbial P content.
Results Wheat growth was suppressed with the addition of residues to the soil, with P uptake closely related to shoot growth. The residue-P contribution ranged between 5 and 52% of the P taken up by wheat plants. The amount of P transferred from the residues to the wheat ranged between 6 and 15% of total residue P. Microbial P increased 2-fold in the low- and moderate-P soils with the addition of residues.
Conclusions The transfer of P from break-crop residues to the wheat plant (as % total residue P) is small in the short term regardless of residue quality and soil P status but incorporating residues increased the microbial P uptake in low- and moderate-P soils.

Key words: ^{32}P isotope, break crops, C-to-P ratio, crop rotation, microbial P, plant P uptake

Introduction

Wheat plants can benefit from legume break crops introduced into the crop rotation (Nuruzzaman et al. 2005). The benefits are attributed generally to nitrogen enrichment, and to disease break effects due to a lowering of the wheat pathogen burden in the soil during the legume phase (Kirkegaard et al. 2008). Grain legumes might also improve the availability of P for a subsequent wheat crop if they are able to mobilise and take up P from non-labile soil P fractions that are not available to wheat. There are several reports that P-efficient legume species have the capacity to mobilise P from sparingly soluble soil P pools (Braum and Helmke 1995; El Dessougi et al. 2003; Gardner et al. 1983; Hocking et al. 1997; Marschner et al. 1986; Vu et al. 2010). It is possible that some of this mobilised P might be made available to a following wheat crop after the decomposition of the legume plant residues.

The transfer of P from break crop residues incorporated into the soil to following cereal plants, has been studied under controlled conditions (Blair and Boland 1978; Fuller et al. 1956; Mat Hassan et al. 2012b; Umrit and Friesen 1994) and also in the field (McLaughlin et al. 1988). The general finding is that the P transfer is low and is quite variable. For example, it has been found that P transfer to following plants generally range from 2 to 20% (Maltais-Landry and Frossard 2015; McLaughlin and Alston 1986; Umrit and Friesen 1994). This low and variable transfer rate could be due to variable P concentrations in the crop residues, which depend on the soil P status, the physiological maturity of the residues, and on the extent of the translocation of shoot-P to the developing grain in the break crops (Thibaud et al. 1988). The low and variable rate could also be

related to differences in growth suppression that have been reported to occur when finely ground residues are incorporated into the soil, prior a wheat crop (Hasbullah et al. 2011; Mat Hassan et al. 2012b). Clearly, there are different factors affecting the P transfer rate including the P concentrations in the residue and the P status of the soil, and these combinations of P supply have not been systematically investigated for wheat and break-crop rotations.

Previous studies that have investigated how soil P availability affects the P transfer from crop residues to following crops have used two approaches. The first has been to use different soil types which also differ in soil P availability (Maltais-Landry and Frossard 2015; Thibaud et al. 1988; Umrit and Friesen 1994). However, this creates the problem where other soil properties might confound the results from the differences in soil P availability. The second approach is to add inorganic P fertilizer to the soil with the crop residues. In this case, one or both of these external P sources are labelled with radioactive P isotopes in order to estimate the actual P transfer from the residues (McLaughlin and Alston 1986). In the study described in this paper, an alternative approach is employed. It involves using only the one soil that differs in P status, which has been equilibrated with incremental P applications over long periods of time. This was achieved by collecting soil from different plots in a long-term experiment, where a range of P rates have been added to the soil over a long-time period, allowing sufficient time for the equilibration of the fertiliser P to occur in the different soil P pools (Blair and Boland 1978). The main advantage of this approach is that only one source of additional P would be added to the soil, in this case the crop residues, facilitating the study of P dynamics on the soil-microbe-plant system.

A major complicating issue when crop residues are added to soil is the potential loss of residue P from immobilisation by the soil microbial biomass. Net immobilisation of P by the microbial biomass occurs when the requirements of an active microbial biomass for P are larger than the P supply from the residues, and this will reduce P supply to the following crop. In contrast, net P mineralisation occurs when the release of P from the residues is in excess of the P requirements of the proliferating microbial biomass. Many researchers refer to the C:P ratio as an expression of the residue quality and hence their potential to result in net P immobilisation or mineralisation. It has been proposed that a C:P ratio of 300 is the critical value over which net immobilisation is likely to occur, and <200 leading to net mineralization (Dalai 1977). However, reports in the literature indicate that the critical values of the C:P ratio range from 60 to 700 (Cheshire and Chapman 1996; He et al. 1997; Umrit and Friesen 1994; White and Ayoub 1983). This large spread in the critical values for the C:P ratio could be related to differences in soil types and in P availability in the soils used in those experiments. They could also relate to the intrinsic quality of the residue that may be more or less amenable to microbial breakdown. Thus, there needs to be a more systematic investigation of the role of soil P status and residue type and quality on the potential availability of residue P to the following crop plants.

This study reports on a controlled-environment experiment that investigated how soil P status and residue type and quality impact on the magnitude of the P transfer to wheat plants. The approach taken was to use the common Vertisol cropping soil from north-west Victoria in Australia, where a long-term P fertiliser trial had been carried out over 15 years. Soils from low-, moderate- and high-P plots were collected and used in factorial combination with a series of residues varying in their C:P ratio, state of maturity and plant species. These residues ranged from a vegetative canola with a C:P ratio of 124, to mature chickpea stubble with a ratio of 832. We hypothesised that the magnitude of the P transfer from the incorporated residues to following wheat plants would increase with combinations of increasing levels of labile soil P and increasing P concentrations in the residues.

Materials and Methods

Soil

The soil used in this study was a Vertosol (Isbell 2002) or a Vertisol (FAO-UNESCO 1978) from a long-term experiment run by the International Plant Nutrition Institute (IPNI). The experimental site was at Dahlen Victoria, Australia (36°38'S and 142°08E). The long-term experiment was established in 1996 and N and P fertilizers were then applied annually, in different combinations. The site had been in a canola-wheat-barley-pulse rotation, with oat hay in 2011, with canola being

the last crop grown in 2013, before the soil samples were collected. Soil samples were collected in 2014 from the 0-15 cm topsoil layer from the plots that had received 80 kg N ha^{-1} $year^{-1}$ applied as urea, and either 9, 18 or 36 kg P ha^{-1} $year^{-1}$ respectively, applied as triple superphosphate. The P was applied up to 2012 when applications to these plots were withheld. Selected properties of the soil are presented in Table 1.

Plant residues

Vegetative canola, chickpea and white lupin, and mature canola and chickpea crop residues were collected from field trials in South Australia, oven-dried at 70°C for 36 h, coarsely ground and passed through a 2 mm sieve. Total P content was determined after acid digestion using concentrated HNO_3 (65%) and a microwave oven (Anton Paar Multiwave 3000). The P concentration in the digests was determined using ICP-OES (Perkin Elmer Optima 8000). Total C and N were determined in an elemental analyser (Perkin Elmer Series II 2400 CHNS/O). Basic properties of the residues are shown in Table 2.

Experimental set-up

A soil mass equivalent to 1 kg of dry-soil was used in each pot. Pots had a 122 mm diameter at the top, and a 104 mm diameter at the bottom, with a height of 140 mm. The total volume was 1,407 cm^3. A head space of 2.5 cm was left from the top, giving an effective soil volume of 1,122 cm^3 and an area of 110.8 cm^2 at the soil surface. Pots were not freely drained. All soils were supplied with basal nutrients added as a P-free stock solution at the following rates (mg kg^{-1} soil): K 67.3, Ca 71.5, S 36.9, Mg 4.9, Mn 1.95, Zn 1.82, Cu 1.53, B 0.12, Na 0.03, Mo 0.07. Nitrogen was applied as NH_4NO_3 and $Ca(NO_3)_2.4H_2O$ at 100 mg N kg^{-1} soil (NH_4:NO_3-N ratio 1:3) initially and then repeated in weeks 3 and 5.

The soil was labelled with a ^{32}P solution in the form of $H_3{}^{32}PO_4$ (Perkin Elmer Inc, Boston Massachusetts 02118, USA) with 0.5 mg P L^{-1} as carrier in order to reduce adsorption of ^{32}P on glassware and guarantee quantitative transfer (Olsen and Sommers 1982). A 10-ml solution containing 0.37 MBq ml^{-1} was added to 1 kg of dry soil equivalent, resulting in an activity of 3.7 Mbq kg^{-1} soil. The soil was then thoroughly mixed and allowed to equilibrate for 10 days at 80% field capacity and 25°C before incorporating the crop residues.
After 10 days of isotope equilibration, the crop residues were incorporated thoroughly into the labelled soil at a rate of 10 g kg^{-1}, and then incubated for another 10 days at 80% field capacity and 25°C before sowing the plants.

Growing conditions

After the isotope equilibration and residue incubation periods, 7 germinated seeds of wheat (*Triticum aestivum* L. cv. Yipti) were sown in each pot. Seven days after emergence, seedlings were thinned to 3 plants per pot. Pots were watered to 90% field capacity by weight every second day during the first 4 weeks and then daily until harvest. Pots were kept in a controlled-environment room (CER). Light in the CER was set to deliver 450 µmol $m^{-2}s^{-1}$ for a period of 14 h with a 10-h dark period, and temperatures were set to 20°C for the day and 18°C for the night.

Measurements

Plant P uptake

The shoots of all pots were harvested after 6 weeks of growth and then oven-dried at 70°C for 72 h, and the shoot dry biomass recorded. Shoots were then ground using a Retsch ZM 200 grinder with 0.5-mm mesh, and subsamples were digested in concentrated HNO_3 (65% w/v) using a microwave oven (Anton Paar Multiwave 3000). The P concentration in the digests was determined using an ICP-OES (PerkinElmer Optima 8000). Shoot P uptake in mg $plant^{-1}$ was calculated by multiplying the shoot biomass by the shoot P concentration. The ^{32}P activity in the digests was measured in a liquid scintillation counter (Tri-Carb 2000 CA, PerkinElmer with QuantaSmart™

software) using Ultima Gold™ XR (PerkinElmer) scintillation cocktail with a ratio 1:6 of digest to cocktail (2 ml sample in 10 ml cocktail). All readings were corrected for radioactive decay back to day 0. No quenching correction was necessary in this study. QuantaSmart™ has a pre-defined assay, called the direct DPM (disintegrations per minute) assay, that performs the DPM calculation based on the quenching indicating parameters SIS (Spectral Index of the Sample) and tSIE (transformed Spectral Index of the External standard). Since this assay is predefined as part of the system, there was no need to define individual parameters and it calculates accurate DPM values for single label beta nucleotides like ^{32}P.

Microbial biomass P

Hexanol-released P was used as a proxy for microbial biomass P. This was determined by the simultaneous liquid fumigation with hexanol and extraction with anion-exchange resin membranes (AMI-7001S Membranes International, New Jersey USA), measuring 6 cm x 2 cm, in the bicarbonate form, as described by Kouno et al. (1995) and subsequently modified by Bünemann et al. (2004b). The P concentrations in the extracts were determined by the malachite green method according to D'Angelo et al. (2001). No correction for P sorption was necessary as the recovery of spiked samples was over 90% in a preliminary test. The microbial P was calculated as the difference between fumigated and non-fumigated extracts with no conversion factor (kp) used.

Calculations

The L value, which is an equivalent measure of the plant-available P pool in the soil, was calculated using the following equation (Frossard et al. 2011):

$$\mathrm{L} = \mathrm{R}/\mathrm{SA}_{\mathrm{plant}} \quad (1)$$

Where *R* is the total amount of radioactivity introduced in MBq kg^{-1} soil and SA_{plant} is the specific activity in the plant, defined as the ratio between the amount of radioactivity recovered in the plant and the amount of ^{31}P taken up by the plant after correction for P derived from the seed. In this case, it was assumed that 40% of the total 130 μg P seed^{-1} was translocated to the shoots, based on this amount being measured in the study by Wang et al. (2011), who used a sand-growing medium with P-free nutrient additions to determine the translocation of seed-P to the shoots in wheat plants. Pypers et al. (2006) showed that the transfer of P from the seed to the shoots of maize and cowpea varied from 40% to 90% for low-P and high-P soils, respectively. However, this variation only had a small effect on the L-value and %Pdfr calculations for the wheat grown in the high-P soil in this study.

The contribution of P from crop residues to the wheat plant was calculated using the following equation (Frossard et al. 2011):

$$\%Pdfr = 100(1 - \mathrm{SA}_{\mathrm{res}}/\mathrm{SA}_{\mathrm{ctl}}) \quad (2)$$

where %Pdfr is the percentage of P in the wheat plant that is being derived from the residues, SA_{res} and SA_{ctl} are the specific activities of the wheat shoots grown on residue-amended soils and non-residue control, respectively. Importantly, this equation assumes that the residues are the only source of ^{31}P diluting the ^{32}P in the soil. The basis for this assumption will be outlined later in the discussion.

Statistical analysis

The data were analysed using two-way analysis of variance (ANOVA), using crop residues and soil P status as factors, to detect the existence of treatment differences at $p \leq 0.05$. Tukey's multiple range test was then used to identify significant differences between treatment means.

The data were checked prior to conducting ANOVA to ensure that they were normally distributed and that the variances were homogeneous. Data transformations were undertaken as necessary when one of these conditions was not achieved. The statistical software used was Genstat 64-bit Release 17.1 (PC/Windows 7) from VSN International Ltd.

Results

Shoot biomass

Soil P status significantly (p<0.001) affected shoot biomass, after 42 days of growth, with biomass increasing as soil P status increased (Fig. 1). Similarly, there was a significant main effect for residues (p<0.001) with shoot biomass generally decreasing with the more mature residues containing lower P concentrations. The largest shoot biomass was produced with the non-residue control and the vegetative canola residue treatments while the mature canola and chickpea residue treatments had the smallest biomass (Fig. 1).

Importantly, there was a significant (p<0.001) residue x soil-P interaction for the shoot biomass. The basis for this interaction was the lower shoot biomass with vegetative chickpea and lupin residues, compared to the non-residue and vegetative canola residues, occurring in the low-P soil, but no differences occurred between these treatments in the moderate-P and high-P soils. Also, the large reduction in shoot biomass with the mature chickpea and canola residues, of around 50%, that occurred in the low-P soil, diminished with increasing soil P status, to a less than 20% reduction in the high-P soil.

P concentrations in wheat shoots and P uptake

The P concentration in wheat shoots was significantly (p<0.001) affected by soil P status, with the average P concentration increasing from 1.9 for the low-P soil to 2.7 mg g^{-1} for the high-P soils (Fig. 2). Wheat plants were somewhat deficient in the low-P soil but not in the moderate- and high-P soils, as indicated by the critical P concentrations in wheat shoots at 42 days.

There was also a significant main effect of residues on shoot P concentrations (p=0.003), with the highest concentration occurring with the vegetative canola residues and the lowest with vegetative lupin and mature canola residues (Fig. 2). However, there was no significant difference in shoot P concentrations between the non-residue control and residue treatments. In addition, there was no interaction between the residue and soil P treatments (Fig. 2).

The treatment effects on shoot P uptake closely followed their effects on shoot biomass (Fig. 1). The P uptake increased with soil P status (p<0.001). The main effects of residues on P uptake paralleled those on shoot biomass with the exception that the P uptake for mature canola residues was significantly less than that for the mature chickpea residues.
There was an interaction between residues and soil P status for shoot P uptake (p<0.05). The basis for this interaction was the higher P uptake with the vegetative canola residues, compared to the non-residue control, which occurred only in the high-P soil. There was also an increase in the P uptake with the vegetative lupin residues relative to the non-residue controls, with increasing P status; the lower P uptake in the vegetative lupin treatment was only significant (p<0.05) for the low-P soil. Finally, the reduction in excess of 60% in shoot P uptake with the mature canola residues, compared to the non-residue control, in the low-P soil, diminished with increasing soil P status, to around 25% reduction in the high-P soil.

Specific activity in wheat shoots, soil labile P pool and microbial biomass P

The specific activities of ^{32}P (SA) in the shoots of wheat plants and in the soil labile-P pool (Resin P) were affected significantly by the soil P status and the residue treatments (Table 3). Thus, increasing the soil P status and the P content in the crop residues both decreased the SA in wheat shoots. The significant soil P status x residue interaction resulted from the large decrease in SA in the low- and moderate-P soils with the vegetative residues, while in the high-P soil there was no difference across the residue treatments.

Similar to that in the shoots, the SA in the soil labile P pool (Resin P) was affected by the addition of residues and the soil P status (Table 3). Thus, increasing the soil P status and the P content in the crop residues both decreased the SA in the soil labile P pool. The significant soil P status x residue interaction resulted from the large decrease in SA in the low- and moderate-P soils with the vegetative residues, while in the high-P soil there was no difference across all residue treatments.

Estimated contribution of residue-P to the P uptake by wheat

The residue-P taken up by wheat shoots, expressed as proportion of P derived from residues (%Pdrf) in Table 4, was affected significantly (p<0.001) by the residue type and soil P status. Thus, increasing the soil P status and decreasing the P concentration in the residue both decreased the relative contribution of residue P to the P uptake by wheat. The basis for the significant (p<0.05) interaction between residue type and soil P status was the larger contribution of vegetative canola residue to the P uptake of wheat, compared to the vegetative chickpea. The amount of residue P, expressed as milligrams of residue P per plant (Table 4), to the P taken up by wheat shoots, was also affected by the soil P status and residue type. Thus, decreasing the P content in the residue decreased the amount of residue P taken up by wheat shoots. Increasing the soil P status, increased the amount of residue P that wheat shoots took up. However, there was a significant (p<0.001) residue x soil-P interaction and this resulted from the high-P soil increasing the amount of residue P taken up by wheat from the vegetative canola and chickpea residues. Soil P status did not affect the amount of residue P taken up by wheat from the vegetative lupin, and mature canola and chickpea residues.

Similar results occurred for the measure of the amount of P recovered from the residues in wheat shoots, (Prfr in Table 4, expressed in mg P plant^{-1}). The soil P and residue main effects, and the soil P x residue interaction were all highly significant (p<0.001) for the Prfr measure. The significant soil P main effect resulted from a higher P recovery of residue P being taken up by wheat from the high-P soil, compared to the low-P soil. Similarly, the residue main effect resulted from the higher P recovery by wheat from the mature chickpea residues, compared to the vegetative canola and vegetative chickpea residues. Most importantly, the soil P x residue interaction was due to a higher P recovery of residue P from mature chickpea residue than from mature canola residue in the high-P soil. There were no differences in the P recovery by wheat from these two residues in the low-P and the moderate-P soils.

The treatments significantly affected the P taken up from labile P pool in the soil (Table 4). The main effect of soil P status resulted from significantly (p<0.001) more P being taken up by wheat from the soil labile P pool as the soil P status increased. The highly significant residue main effect (p<0.001) resulted from more P being taken up from the labile soil P pool when vegetative canola and vegetative chickpea residues were added, compared to when mature canola residues were added. There was no significant soil x residue interaction for the P taken up from the soil labile P pool.

Soil P availability

The *L* value gives a measure of the soil available P pool that plants had access to during the 42 days of growth (Fig. 3). The values were significantly affected (p<0.001) by the soil P status and residues, with *L* values increasing with increasing soil P status and with increasing P concentration in the added residues. The increment in *L* value, above that for the non-residue control, was positively related to the total amount of P added initially to the soil in the residues (r=0.95).
A significant soil P x residue interaction (p<0.05) occurred for the *L* values. The basis of this interaction was that the *L* value was similar for the vegetative chickpea and canola residues in the high-P soil while it was lower for the vegetative chickpea than the vegetative canola residue in the moderate- and low-P soils.

Microbial biomass P

The added residue treatments had very similar effects on microbial biomass P (Hexanol-released P) in the low- and moderate-P soils (Fig. 4). The values for each residue treatment increased above the microbial-P value for the non-residue control as a significant main effect. The interaction between the residue and soil P status was also significant (p<0.05). The basis of this interaction was that in the low-P soil with the vegetative lupin residues, the microbial P was more than twice of that in the non-residue control. In the moderate-P soil, the non-residue control had the lowest microbial P compared to all the crop residue treatments. There were no differences in the microbial P between the residue treatments and the non-residue control in the high-P soil.

Discussion

Treatment effects on the growth of the wheat plants

Adding mature crop residues to the Vertisol soils in this study resulted in the growth suppression of the wheat plants. The suppression depended on the C:P ratio of the residue and the P status of the soil, with all residues apart from the vegetative canola with the lowest C:P ratio of 124, resulting in significant reductions in shoot biomass in the low-P soil (Fig. 1). This suppression in growth of wheat plants, when crop residues are incorporated in soil, has been reported previously. For example, Mat Hassan et al. (2012b) reported the reduction in wheat growth by up to 72% compared to the non-residue control when they added white lupin residues with a C:P ratio of 232 in a sandy soil low in available P (resin P of 4.5 mg kg^{-1}). Earlier, McLaughlin and Alston (1986) reported a reduction of 45% in wheat growth relative to the control with the addition of labelled medic residues to a sandy soil low in P availability (0.3 mg P kg^{-1} $NaHCO_3$-extractable P). On the other hand, other studies have reported increases in wheat growth by 60% when green-manure-type residues with very high-P concentrations of 6.5 mg P g^{-1} were incorporated to a sandy soil low in P availability (resin P of 4.5 mg P kg^{-1}) prior to growing the wheat (Hasbullah et al. 2011). On face value, given the link between soil P status and the extent of the growth reduction, the suppression in wheat growth in this study could be related to a limiting P supply for the wheat plants, when added residues were low in P and the soil had a low-P status. An accepted explanation for this P deficiency, put forward by McLaughlin and Alston (1986), Oberson and Joner (2005) and Marschner (2008), is that P in the soil is being immobilised by the microbial biomass.

It is unlikely that the suppression in the growth of the wheat plants with mature crop residues was due solely to P deficiency, induced by the immobilisation of P by the microbial biomass. The shoot P concentrations in the wheat plants grown on the low-P soils were low, at around 1.8 to 1.9 mg P kg^{-1} (Fig. 2) and were likely to limit the growth as these were below the reported critical P concentration of around 2.2 mg P kg^{-1} (Reuter et al. 1997) for wheat at this stage of growth. However, there were no large, significant reductions in shoot P concentration when mature crop residues were added to the low-P soil, compared to the non-residue control as there was no significant soil P x residue interaction in Fig. 2, which contrasts with the large reductions in shoot biomass when the mature residues were added to the low-P soil (Fig. 1). Furthermore, the wheat plants still experienced a 27% reduction in shoot biomass with mature canola residues added to the high-P soil, compared to the non-residue control; yet the P concentration in their shoots was 2.6 mg P kg^{-1} (Fig. 2) which was above the critical P concentration for wheat at this stage of growth. Also, the wheat shoots were unlikely to be limited by a low-N supply resulting from microbial immobilisation, given the regular N applications to the soil and the relatively adequate N concentrations in their tissue (Fig. S1). This reason is supported by the work of Hasbullah et al. (2011) and Mat Hassan et al. (2012a) who reported P and N concentrations in wheat plants, following the incorporation of mature residues in the soil. The P concentrations in plants were above the critical P concentrations for their wheat plants. Thus, the reduced wheat growth in their study, following the addition of residues, cannot be attributed to P or N deficiency.

A further line of evidence that argues against the growth suppression being cause by P deficiency comes from the *L* values in Figure 3. The *L* value is a measure of the size of the plant-available soil P pool, based on the specific activity in the plant shoots. The small non-significant increases in *L* values with the addition of the mature residues, above those of the non-residue controls, suggest that the size of the labile P pool in soil, that is available to plants, was not decreased with the addition of these residues (Fig. 3). Some of the P in the residues was released into the soil solution diluting its specific activity, which it is then reflected in the P taken up by the plants, resulting in increased *L* values. The *L* values were further confirmed by the *E* values calculated at the time of the harvest (Fig. S2). The *E* value is a direct measure of the soil labile P pool, based on the specific activity of the resin P. In this case, the ratio between *L* and *E* was very close to 1 for all treatments, indicating that the P from residues entered mainly into the soil available P pools where plants sourced their P with no additional mobilisation form non-available P pools. This reinforces the proposition that P deficiency is not solely responsible for the plant growth suppression and hence the reduced P uptake by wheat plants.

The issue remains as to what is contributing to the growth suppression of the wheat. One alternative explanation could be the allelopathic effects of some toxic compound(s) that might be released during the decomposition of the mature crop residues. Such compounds have been reported to inhibit the early growth of the wheat plants (Barnes and Putnam 1986; Barnes et al. 1987; Jessop and Stewart 1983; Lynch et al. 1981). Lynch et al. (1981) and Jessop and Stewart (1983) focused their studies on the effects of the crop residues on the early growth of wheat and reported that the growth suppression was due to production of phytotoxic compounds during the decay of the residue material. Barnes and Putnam (1986) and Barnes et al. (1987) worked with cereal rye and isolated the toxic compounds as benzoxazinones which were responsible for the negative effect on the radicle elongation. Further research is needed to fully understand how the addition of residues of break crops to the soil, affect the growth of following wheat plants.

Treatment effects on the P nutrition of the wheat plants

The total P uptake by wheat shoots closely reflected their biomass, and in general related more to the soil P status (Fig. 1). However, the source of the P taken up by the wheat shoots, from either the labile P pools in the soil or from the residues, varied across soil and residue treatments (Table 4). The quantity of residue P taken up by the wheat shoots was closely related to the P concentration in the residues and these amounts were surprisingly constant across all soils. In contrast, the quantity of soil labile P in the wheat shoots was more related to soil P status, and this increased as the soil P status increased. It is understandable that the soil P status directly affects the P taken up from the labile P pool, as the soils with a higher P status have a larger plant-available P pool by definition, and this labile P exchanges with the ^{32}P added at the beginning of the experiment. Similarly, the higher P concentrations in the vegetative crop residues, with a higher, rapidly releasing, inorganic Pi fraction, compared to the slower-releasing organic Po fraction (Noack et al. 2012), means that these vegetative residues will provide more P in the short term, than the mature residues. It is therefore not unexpected that higher residue-P uptake by the wheat shoots occurs with the high-P, green-manure-type, vegetative residues, compared to the mature residues.

The specific activity of ^{32}P in the wheat shoots was lower in the residue treatments, compared with the non-residue control treatments for the three soils (Table 3), with the effect being more marked for the low-P soil. It is tempting to draw the conclusion that this decline in the specific ^{32}P activity between non-residue control and residue treatments was caused by the dilution with ^{31}P released from the residue tissues. This assumption using the indirect labelling technique to quantify the contribution of residues to the P nutrition in plants has been made before (Maltais-Landry and Frossard 2015; Thibaud et al. 1988; Umrit and Friesen 1994). However, it cannot be ruled out that some of the ^{31}P might be released from the mineralisation of endogenous soil organic matter, or the mineralisation of P from the microbial biomass, or indeed from dissolution of some sparingly-soluble inorganic ^{31}P sources in the soil. The reason behind this stems from the recent advances in the understanding of 'carbon priming' when organic matter is added to the soil (Fontaine et al. 2003; Kuzyakov 2010; Pascault et al. 2013) and the stimulation of the microbial biomass in the soil to mineralise the endogenous soil organic matter (Bingeman et al. 1953; Hallam and Bartholomew 1953). It is possible then that some of the soil's endogenous organic matter in this study was mineralised by the increase in growth and activity of the soil microbial communities, stimulated by the addition of labile C in the residues. This in turn made more non-labile ^{31}P available to the plants. Moreover, because of the competition between microbes and plants for the labile P in the soil, then additional mechanisms, such us rhizosphere priming, might well come into play (Dijkstra et al. 2013). Notwithstanding all of the above, the close relationship between the amount of residue-P added to the soil and the P uptake from residues in Table 4, suggests that much of the P taken up by the plants is being supplied from the added residues. Therefore, the cautious assumption is made that the P in wheat shoots not derived from labile soil P represents an estimate of the maximum possible P that comes from the incorporated residues.

Using the assumptions outlined above, the estimated P transfer from the crop residues to the wheat plant (as % total residue-P) was small in this short-term study. Both mature and vegetative residues added to the soils resulted in P transfers between 6 and 15% (Table 4) of the

total P added with residues. The maximum relative P transfer occurred with the mature chickpea residues in the high-P soil, whereas the lowest occurred with the vegetative chickpea in the low-P soil. Thus there was no consistent pattern for the relative P transfer from the residues to the wheat shoots with minimal effects from the soil P status or from the P concentration in the residues. These results are consistent with those from earlier studies (Maltais-Landry and Frossard 2015; Mat Hassan et al. 2012b; McLaughlin and Alston 1986; Nachimuthu et al. 2009; Noack et al. 2014) which used finely ground residues incorporated in the soil. They found the residue contribution to P uptake, in the short term, was up to 20% of the total P introduced in residues. This transfer of P from the residues to the wheat plants is the end-result of three processes. One is the release rate of P from the residue, governed by the decomposition rate. Second is the extent of the microbial immobilisation and/or soil adsorption/precipitation that removes this released P from the soil solution. But it is also influenced by the growth suppression experienced by the plants after residue incorporation. Despite the fact that the transfer of P from incorporated residues to the following crop is small in the short term, it might become larger for subsequent crops in the rotation, following the turnover of the microbial populations that take up the P in the short term. Unfortunately, the short half-life of the radioactive ^{32}P isotope limit the experimental opportunities to measure these fluxes of P in the longer term.

Treatment effects on the microbial biomass P

In contrast to the P uptake by wheat shoots, the addition of vegetative and mature crop residues increased microbial P uptake (hexanol-released P) (Fig. 4). Interestingly, there were minimal differences in the effect of residues on the microbial P, despite the wide range of P concentration (0.5 to 3.3 mg g^{-1}) in the residues with C:P ratios varying from 125 to 832. Yet all the residue treatments applied to the low- and moderate-P soils resulted in an extra 5 to 11 mg P kg^{-1} soil in the microbial P, over their respective non-residue controls. What was constant was the amount of C added in the residues, which was 4.1 g C kg^{-1} soil. This indicates that the addition of this C to the soil resulted in generally similar responses by the microbial biomass in terms of their P uptake. Thus, the microbial biomass was able to take up around the same amount of P with the addition of mature crop residues in the low-P soil, compared to that taken up when vegetative residues were added to the moderate-P soil, highlighting the capacity of the soil microbial biomass to acquire P, when they are supplied with sufficient C and N. This is the conclusion of many researchers who have found that the microbial biomass and its uptake of nutrients, increases in proportion to the amount of C added in crop residues, given that the availability of C substrates is the important limiting factor for microbial proliferation in agricultural soils (Bünemann et al. 2004a; Marschner 2008; Oberson and Joner 2005; Veen et al. 1984)

The amount of P taken up by microbes in the most P-limiting treatments is of special interest. Mature canola and chickpea residues that were added to the soils provided around 5.5 mg P kg^{-1} soil. According to the estimates from the literature (Damon et al. 2014; Noack et al. 2012; Oberson and Joner 2005), about half of this P (2.25 mg kg^{-1} soil) is in an inorganic, readily-available P form that is released rapidly into the soil solution. Around another 0.15 mg-P kg^{-1} soil would be released from the remaining organic and recalcitrant P forms in the residues within the experimental period at a suggested rate of 0.02 mg kg^{-1} soil $week^{-1}$ (Damon et al. 2014). Thus a total of around 2.4 mg kg^{-1} soil would be released from these mature residues during the period of this experiment. Of this P, wheat shoots acquired around 0.45 mg kg^{-1} soil. So at best there would still be around 2.0 mg kg^{-1} soil released from crop residues, yet the additional microbial P in the mature-residue treatment in the low-P soil, over and above that for the non-residue control, was 6.6 mg kg^{-1} soil. The issue is from where the microbial biomass acquired this additional 4.6 mg kg^{-1} soil.

It is not possible in this experiment to determine the exact source(s) of the extra P that was taken up by the microbial biomass in the low-P soil with low-P residues. Some of it might have been from the soil available P (Bünemann et al. 2004b). In addition, some non-labile inorganic P could have been solubilised by the microbes (Guppy and McLaughlin 2009; Nahas 2007; Richardson 2001; 2007). It should be remembered that the soil conditions in this study were quite unique; the microbes were supplied with 4.1 g C kg^{-1} soil, there was no limitation in moisture or N

supply, and temperature was optimum for microbial growth. It would appear that under these conditions, the microbial biomass was not constrained by the low-P conditions, and was able to take up similar amounts of P irrespective of the supply of available P in the low- and moderate-P soils, or the P concentrations in the residues. This further highlights the capability of an unconstrained microbial biomass to acquire soil P to satisfy their requirements under low-P conditions.

Agricultural implications

Although conditions of this experiment are different from the normal field conditions in terms of temperature, moisture and N supply, it is still possible to make some extrapolations to the field situation. For example, the incorporation of mature residues into the soil can cause growth suppression to the immediate following crop in the short term that cannot be explained solely by the microbial immobilisation of nutrients, including N, as N was in adequate supply. Nevertheless, any suppression in the growth of wheat plants is a significant negative outcome. Allelopathy effects from compounds in the residues may provide a mechanism for this suppression. However, further investigation is needed to fully understand the mechanisms and the extent that it might occur under field conditions.

The addition of C in the mature crop residues with high C:P ratios resulted in significant increases in the P uptake by the soil microbial biomass. This led to P immobilisation in the soil, suggesting that additional P fertiliser might be required to sustain plant growth, depending on the soil P status (Damon et al. 2014). Chaves et al. (2004) and Chen et al. (2014) found that a similar situation occurs with N supply, when mature low-N crop residues are added to the soil. This in turn would most likely require additional N fertiliser to be applied to address a short fall in N supply (Hodge et al. 2000). Adding mature crop residues to low-P soils may therefore require the application of N and P fertilisers to maintain crop production. However, a positive aspect may be that the mature crop residues will stimulate the mobilisation of P from non-labile P pools and/or organic P forms by the proliferating microbial communities. This P might then become available to the following crop at some point in time. The issue is the extent of this P mobilisation by the microbes, and the likely timing of any release of mobilised P to the following crops. This is an important research question that requires future investigation.

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Table 1. Basic properties of the soils used in the study

P level	Fertilizer history[1] (kg P $ha^{-1}yr^{-1}$)	Olsen P (μg g^{-1})	Total P (μg g^{-1})	Total C (mg g^{-1})
Low	9	7	143	11.7
Moderate	18	15	172	12.3
High	36	30	191	12.8

[1] The rate of fertilizer added each year started in 1996 and was suspended in 2012, the last crop grown was canola in 2013 and soil samples collected in 2014.

Table 2. Concentrations of P, C and N, and C:P and C:N ratios of the residues used in this study

Residue	P conc. (mg g^{-1})	P added to the soil as residues (μg g^{-1} soil)	C conc. (mg g^{-1})	N conc. (mg g^{-1})	C:P	C:N
Vegetative						
Canola	3.3	33	413	20.4	125	20.1
Chickpea	2.3	23	413	18.8	179	21.9
White lupin	1.6	16	406	12.5	266	34.1
Mature						
Canola	0.6	6	405	5.1	675	79.5
Chickpea	0.5	5	416	8.5	832	49.1

Table 3. The effect of residue treatment and soil P status on the specific activity (SA) of wheat shoots and, soil resin P after 42 days of growth.

Means followed by a same letter are not significantly different (p>0.05) using the Tukey's test.

	SA wheat shoot[1] (kBq ^{32}P mg^{-1} ^{31}P)	SA soil resin-P[2] (kBq ^{32}P mg^{-1} ^{31}P)
Low-P soil		
Non-Residue	114.3 ^{i}	91.7 ^{fg}
Canola Veg	55.4 ^{cde}	61.9 ^{def}
Chickpea Veg	68.7 ^{ef}	73.6 ^{efg}
Lupin Veg	75.5 ^{fg}	74.6 ^{efg}
Canola Mat	89.1 ^{gh}	85.4 ^{fg}
Chickpea Mat	92.7 ^{h}	106.6 ^{g}
Moderate-P soil		
Non-Residue	70.8 ^{f}	60.1 ^{def}
Canola Veg	47.0 ^{bc}	45.5 ^{bcd}
Chickpea Veg	56.0 ^{cde}	49.8 ^{cde}
Lupin Veg	54.4 ^{cd}	76.9 ^{efg}
Canola Mat	62.9 ^{def}	70.5 ^{defg}
Chickpea Mat	64.0 ^{def}	72.2 ^{defg}
High-P soil		
Non-Residue	38.1 ^{ab}	30.1 ^{ab}
Canola Veg	28.1 ^{a}	30.5 ^{ab}
Chickpea Veg	30.0 ^{a}	31.6 ^{abc}
Lupin Veg	34.0 ^{ab}	28.1 ^{a}
Canola Mat	36.3 ^{ab}	36.4 ^{abc}
Chickpea Mat	35.3 ^{ab}	33.1 ^{abc}
Significance level (p)		
Soil P (P)	<0.001	<0.001
Residue	<0.001	<0.001
P x Residue	<0.001	0.031

[1] SA in wheat shoots was corrected assuming 40% of seed-P transferred to the shoots after 42 days of growth

[2] Data were log_{10} transformed before ANOVA.

Table 4. Estimated amount of P taken up by wheat shoots from added residues to the soil. Means followed by a same letter within each column do not differ significantly (p<0.05), as determined by the Tukey's multiple range test.

	P derived from residues (%Pdfr)	P recovered from residues[1] Prfr (mg plant^{-1})	P from residues recovered in wheat shoots[2] (%)	P derived from soil labile P pools[3] (mg plant^{-1})
Low-P soil				
Non-Residue	-	-	-	1.62
Canola Veg	51.6 ^{i}	0.88 ^{f}	8.0 ^{abcd}	0.82
Chickpea Veg	39.9 ^{hi}	0.45 ^{cde}	5.8 ^{a}	0.67
Lupin Veg	33.9 ^{gh}	0.32 ^{abcd}	6.1 ^{a}	0.62
Canola Mat	22.0 ^{def}	0.14 ^{a}	6.9 ^{ab}	0.48
Chickpea Mat	18.9 ^{bcde}	0.13 ^{a}	8.0 ^{abcd}	0.58
Moderate-P soil				
Non-Residue	-	-	-	2.61
Canola Veg	33.6 ^{fgh}	0.97 ^{f}	8.8 ^{abcd}	1.92
Chickpea Veg	21.0 ^{cde}	0.59 ^{e}	7.6 ^{abcd}	2.20
Lupin Veg	23.2 ^{efg}	0.53 ^{de}	9.9 ^{abcd}	1.75
Canola Mat	11.1 ^{abcd}	0.17 ^{ab}	8.7 ^{abcd}	1.40
Chickpea Mat	9.7 ^{abc}	0.19 ^{ab}	11.6 ^{de}	1.81
High-P soil				
Non-Residue	-	-	-	3.95
Canola Veg	26.3 ^{efg}	1.22 ^{g}	11.1 ^{bcde}	3.42
Chickpea Veg	21.2 ^{cde}	0.86 ^{f}	11.2 ^{cde}	3.20
Lupin Veg	10.8 ^{abcd}	0.37 ^{bcd}	7.0 ^{abc}	3.09
Canola Mat	4.8 ^{a}	0.14 ^{a}	7.1 ^{abc}	2.82
Chickpea Mat	7.4 ^{ab}	0.24 ^{abc}	14.6 ^{e}	3.06
Significance level (p)				
Soil P (P)	<0.001	<0.001	<0.001	<0.001
Residue	<0.001	<0.001	<0.001	<0.001
P x Residue	0.038	<0.001	0.002	0.270

[1] Prfr is calculated by multiplying the total P uptake in mg plant^{-1} by the %Pdfr. This includes P from residues and non-labile P pools in the soil (see discussion).
[2] This measure is based on the assumption that all the non-labile P accumulated in the wheat shoots came only from the residues (see discussion).
[3] This is the difference between the total P uptake per plant and the P derived from residues.

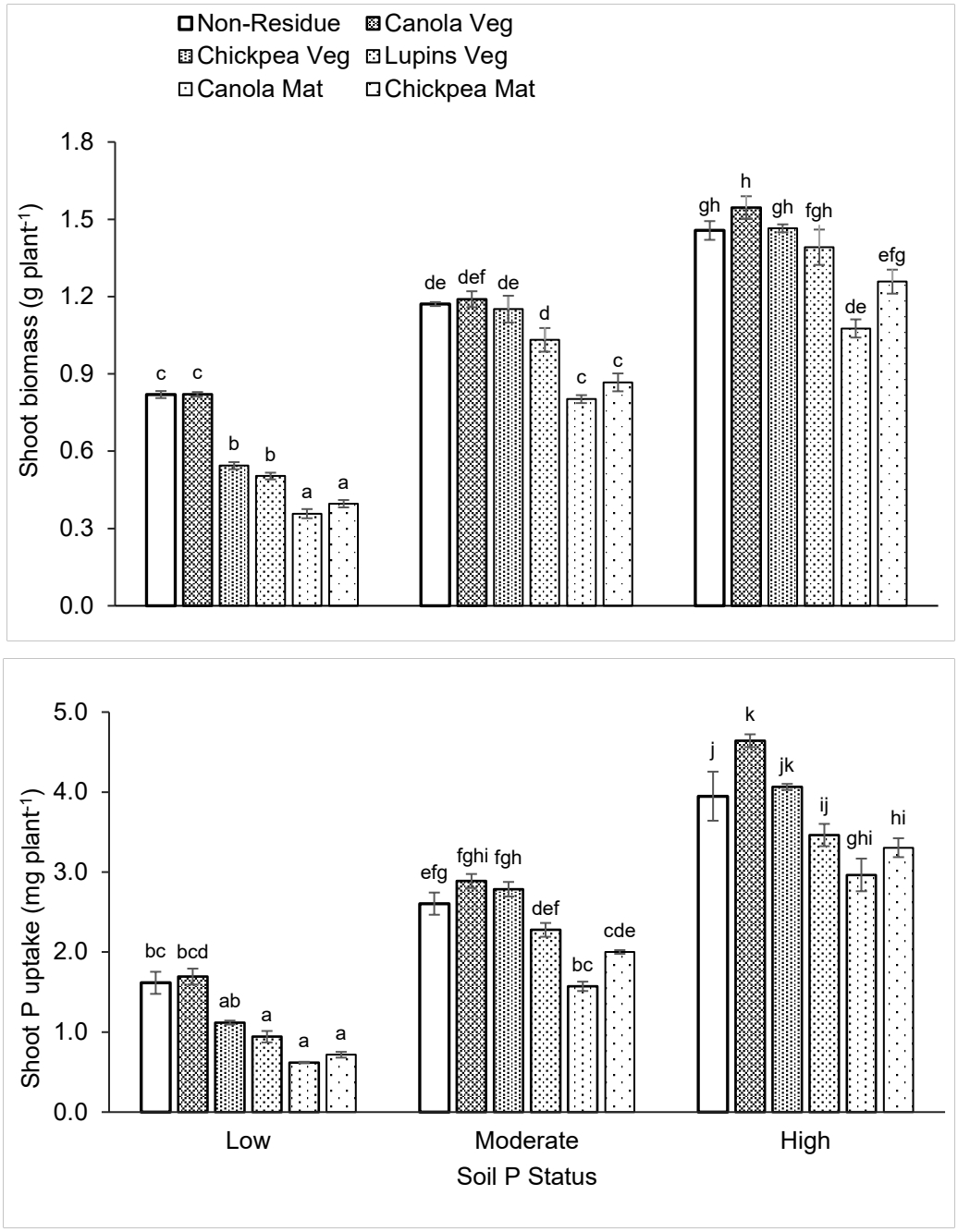

Figure 1. Effects of residue type and soil P status on the shoot biomass and the shoot P uptake of wheat plants after 42 days of growth. Means followed by the same letter do not differ significantly (p>0.05), using the Tukey's test. Error bars represent ± 1 standard error (n = 3) for each individual mean. The effects of soil P status, residue and their interaction are highly significant (p<0.001) for the shoot biomass. The effects of soil P status (p<0.001), residue (p<0.001) and their interaction (p<0.05) are all significant for shoot P uptake.

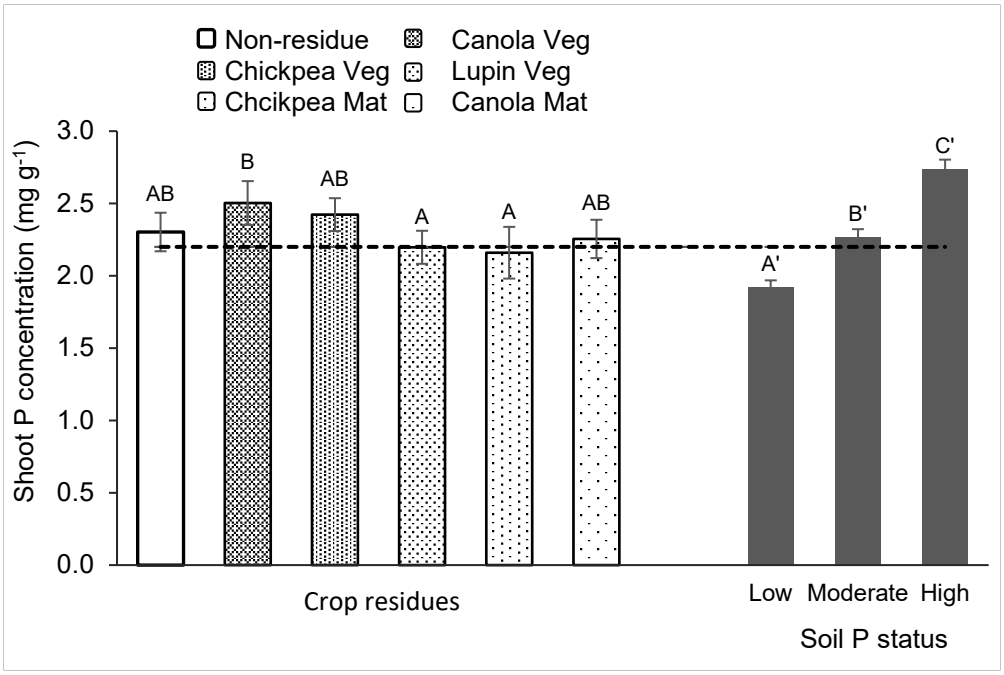

Figure 2. Main treatment effects of crop residue and soil P status on the shoot P concentration in wheat plants after 42 days of growth. Means followed by a same type of letter do not differ significantly, using the Tukey's test. The dotted line indicates the critical P concentrations in wheat shoots during the late vegetative growth (Reuter et al. 1997). Error bars represent ± 1 standard error. The effects of soil P status (p<0.001) and residue (p=0.003) are significant, but not their interaction (p=0.435).

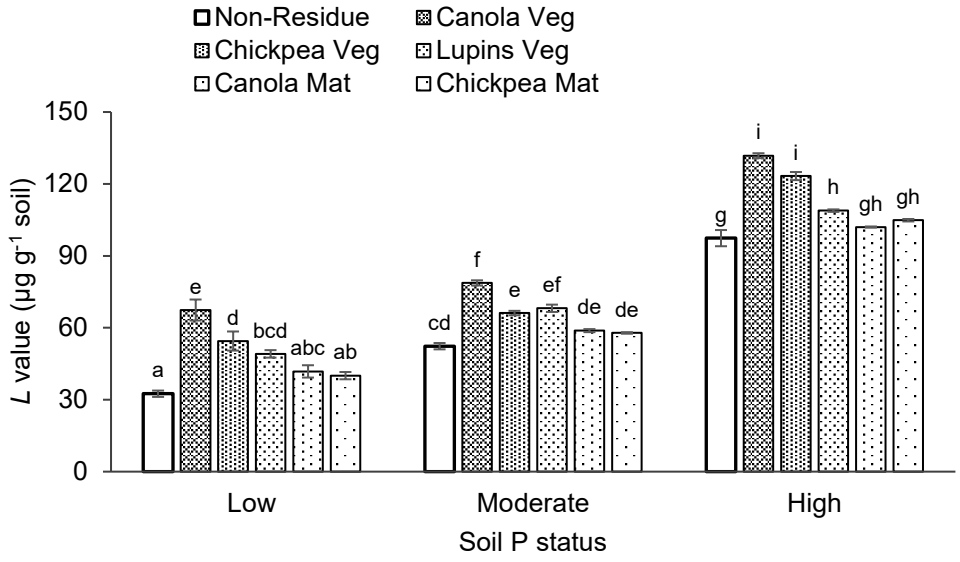

Figure 3. Effects of residue treatment and soil P status on *L* values after 42 days of plant growth. Means followed by a same letter do not differ significantly (p>0.05), using the Tukey's test. Error bars represent ± 1 standard error of the mean (n = 3). The effects of soil P status (p<0.001), residue (p<0.001) and their interaction (p=0.017) are significant.

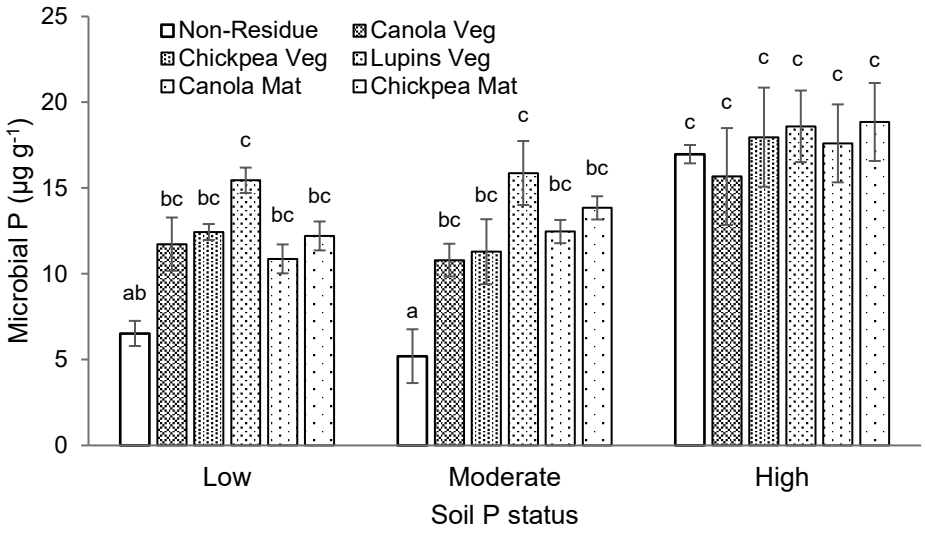

Figure 4. Main effects of residue treatment and soil P status on microbial P (Hexanol-released P) after 42 days of plant growth. Means followed by the same type of letter do not differ significantly (p>0.05) using the Tukey's test. Error bars represent ± standard error of the mean (n = 3). The effects of soil P status (p<0.001), residue (p<0.001) and their interaction (p=0.048) are significant (the data were $\log_{10}$ transformed).

Electronic Supplementary Materials

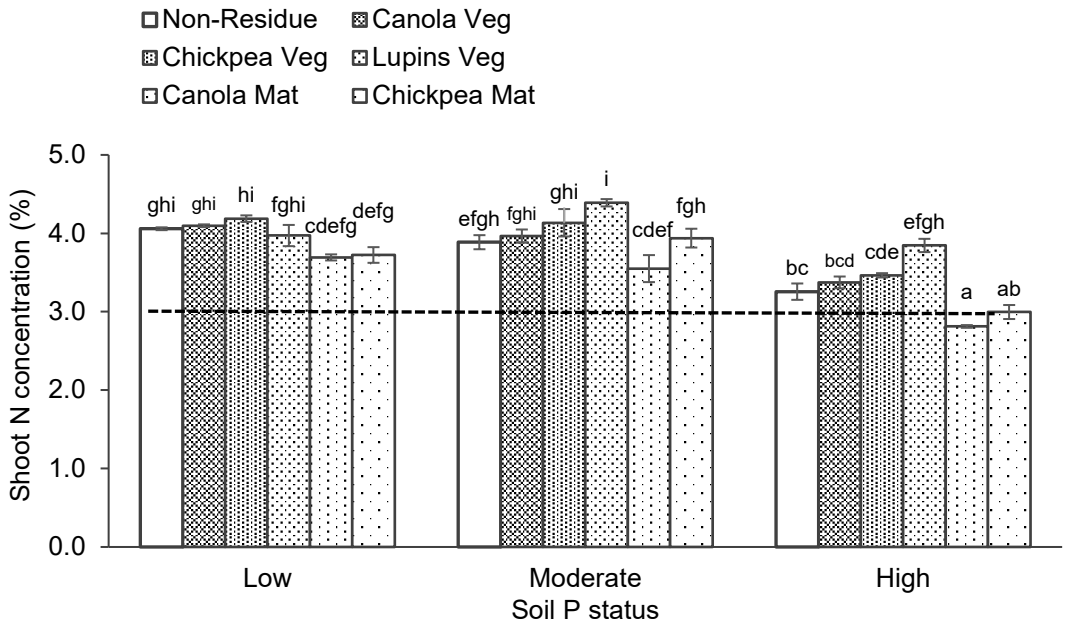

Figure S1. Effects of residue treatment and soil P status on shoot N concertation of wheat plants after 42 days of growth. Means followed by a same letter do not differ significantly (p>0.05), using the Tukey's test. The dotted line indicates the critical N concentrations in wheat shoots during late vegetative growth (Reuter et al. 1997). Error bars represent ± 1 standard error of the mean (n = 3). The effects of soil P status (p<0.001), residue (p<0.001) and their interactions (p=0.020) are significant.

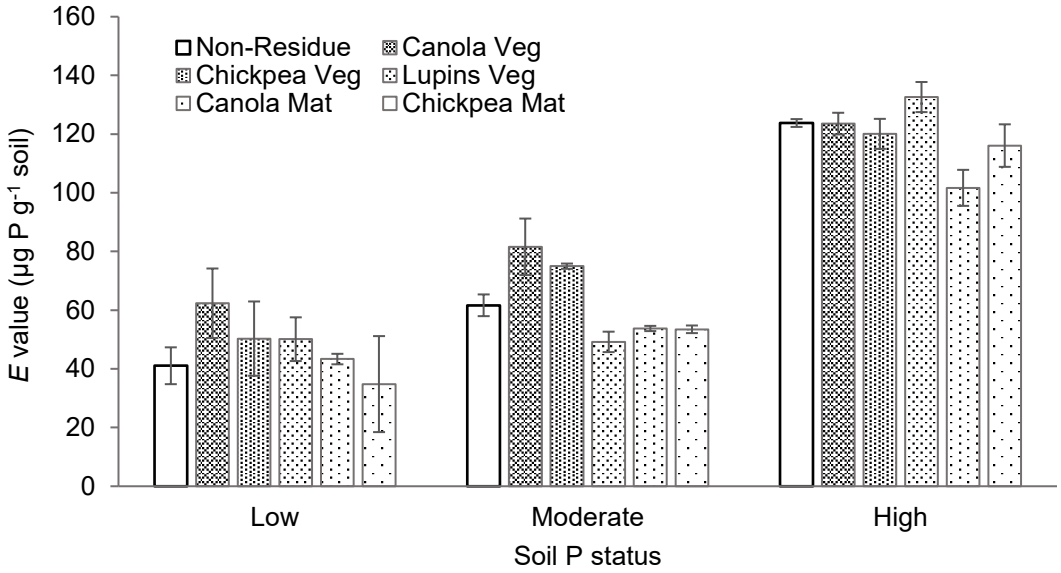

Figure S2. Effects of residue treatment and soil P status on *E*-values after 42 days of plant growth. Error bars represent ± 1 standard error of the mean (n = 3). The effects of soil P status (p<0.001), residue (p=0.003) are significant, but not their interaction (p=0.181). *E*-values (mg P kg^{-1} soil) were measured according to Frossard et al. (2011) and calculated using the following equation:

$$E(t) = VCp(R/r(t))$$

where V is the water to soil ratio (L kg^{-1}), Cp is the concentration (mg L^{-1}) of Pi in the water extract, R is the total radioactivity added to the soil solution (kBq g^{-1} soil) and *r(t)* is the radioactivity (kBq g^{-1} soil) in the resin extract of soil at *t* time.