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Influence of the order in which low and high C/N residues on soil nutrient availability and wheat nutrient uptake

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Summary

It is well-known that the C/N ratio of plant residues can influence soil nutrient availability, but the effect of repeated addition of plant residues with different C/N ratio is less explored. In previous studies, we showed that nutrient availability and soil respiration after the second residue addition is influenced not only by the C/N ratio of that residue, but also by the C/N ratio of the previously added residue. These experiments were carried out without plants and it was unclear how the legacy effect would influence plant growth and nutrient uptake. The aim of this experiment was to assess plant growth, nutrient uptake and soil nutrient availability after the second residue addition with different length of time between the first and second residue addition where the first and second residue had the same or a different C/N ratio. High (H) or low C/N (L) residue was added at the start of the experiment, the second residue with either the same or a different C/N ratio was added on days 7, 14, 21 or 28 with a total residue addition of 20 g kg^{-1} giving four residue treatments: HH, LL, LH and HL. Wheat was planted immediately after the second residue addition and grown for 28 days. N and P availability were measured on days 7, 14, 21 and 28 and at plant harvest. Soil N and P availability after the second residue addition were in the order HH<LH<HL<LL. Wheat biomass generally did not differ between LL, HL and LH, but wheat in HL and LH had a lower shoot/root ratio than in LL suggesting that in HL and LH the plants were able to compensate the lower nutrient availability by increased root growth. In conclusion, the C/N ratio of the previous residue addition influenced nutrient availability after the second residue addition, but plant growth did not differ between HL, LH and L because plants in the former developed a more extensive root system and could therefore access the nutrients released during decomposition of L even in treatments where both H and L were present in the soil.

Keywords: Legacy effect; N availability, P availability; residue C/N ratio; shoot/root ratio; wheat

Introduction

Nutrients in organic amendments are an important source of nutrients for crops (Flavel and Murphy, 2006; Quilty and Cattle, 2011). However, nutrient release cannot be predicted reliably because decomposition of organic amendments and concomitant nutrient release are influenced by environmental factors such as temperature and rainfall which influence microbial activity, soil properties such as nutrient binding capacity and by residue properties, particularly the C to nutrient ratio (Quilty and Cattle, 2011). Nevertheless organic amendments are likely to used more frequently in the future as inorganic fertilizer prices increase (Conyers and Moody, 2009; Cordell et al., 2009; Hargreaves et al., 2008; Quilty and Cattle, 2011).

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Decomposition rate and nutrient release are influenced by the chemical composition of organic soil amendments (Tian et al., 1992b; Vanlauwe et al., 1996a). Water-soluble organic C is quickly decomposed (Hadas et al., 2004), whereas decomposition of lignin is slow (Nwoke et al., 2004). Nutrient concentration of the organic amendment influences not only decomposition rate but also nutrient availability. For example, organic materials with C/N > 20 and C/P > 200 are decomposed more slowly than those with lower nutrient ratios and result in at least temporary net immobilisation as microbes take up N or P from the soil to satisfy their N and P demand (Enwezor, 1976).

These well-known principles are used to predict nutrient release from organic amendments. However, quite often the actual amount and timing of nutrient release differs from that predicted (Freschet et al., 2012; Rashid et al., 2013; Strickland et al., 2009). This suggests that other factors also influence decomposition rate and nutrient release. One such factor is previous management history of the soil, which has been shown to influence soil physical properties, organic matter content, nutrient availability and microbial community composition (Lewis et al., 2014). (Carrillo et al., 2012) found that in the three weeks after the new litter addition, available N concentrations were influenced by both the previous and new litter properties.

In two recent studies, we investigated the legacy effect of the previous plant residue C/nutrient ratio on the microbial activity, biomass and nutrient availability after addition of a second residue with the same or different C/nutrient ratio (Marschner et al., 2015; Nguyen et al., 2016). In this context, the term legacy effect refers to the influence of the first residue on decomposition and nutrient release after the second residue is added. When the second residue was added three weeks after the first, available N and P concentrations 21 days after the second residue addition decreased in the following order: low following low C/N residue > low following high C/N residue > high following low C/N residue > high following high C/N residue (Marschner et al., 2015). Thus, the previous high C/N residue reduced available N concentrations after low C/N residue addition compared to low C/N after low C/N residue. On the other hand, the previous low C/N residue resulted in greater available N concentrations after high C/N residue addition compared to high C/N following high C/N residue. Nguyen et al. (2016) found that when low C/N was added after high C/N residue, the available N concentration after the second residue addition was lower when the second residue was added 10 days after the first than when the interval between residue addition was 30 days. This indicated that the extent by which the legacy effect influences nutrient availability is dependent on time between residue additions.

Our previous studies on the legacy effect were conducted without plants. Therefore it was not clear if the legacy effect influences plant growth and nutrient uptake and if this changes with time between residue additions. The aim of the present study was to assess plant growth, nutrient uptake and soil N and P availability after the second residue addition with different length of time between the first and

second residue addition. The hypotheses were: (1) N and P availability after the second residue is influenced by the legacy effect, i.e., is lower when low C/N residue follows high C/N residue than if low C/N residue follows low C/N residue; (2) the legacy effect on N and P availability will decrease with time between residue additions; (3) plant growth and N and P concentrations after the second residue will be influenced by the legacy effect, i.e., will be greater if high C/N residue follows low C/N residue than if high C/N residue follows high C/N residue, and will be greater with low following high C/N residue than with high following low C/N residue.

Materials and methods

Silt loam soil was collected from 0 - 15 cm at Waite Campus, The University of Adelaide (34°58'S, 138°37'E). The area is in a semi-arid region and has a Mediterranean climate with cool, wet winters, and hot and dry summers. The soil is classified as Chromosol in Australian soil classification (Isbell, 2002), and a Rhodoxeralf in US Soil Taxonomy (Staff, 2014). The soil was managed for over 80 years in the Waite Long-term Rotation trial as permanent pasture. It has the following properties: sand 70%, silt 20% and clay 10%, pH (1:5 soil: water) 7.3, electrical conductivity (EC 1:5) 742 µS cm^{-1}, total N 134 mg kg^{-1} and total P 461 mg kg^{-1}, total organic C (TOC) 15 g kg^{-1}, available N 15 mg kg^{-1}, available P 32 mg kg^{-1}, maximum water holding capacity (WHC) 327 g kg^{-1} and bulk density 1.3 g cm^{-3}. After collection, the soil was dried at 40 °C in a fan-forced oven. In summer, daytime temperatures often exceed 40 °C in the top soil and soils are air-dry for several weeks, therefore this treatment is not unnatural. After drying, visible plant debris was removed and the soil sieved to < 2 mm.

Before the start of the experiment, the soil was pre-incubated for 10 days at 20 °C at 50% of WHC to reactivate the microbes and to stabilise their activity after rewetting. This water content was chosen because Setia et al. (2011) found that microbial activity of a soil of this texture was maximal at 50% WHC which was confirmed in our recent study (Marschner et al., 2015).

After pre-incubation, 400 g moist soil was filled into plastic pots lined with plastic bags. Throughout the experiment the soil water content was maintained at 50% water holding capacity by weighing the pots daily and adjusting the weight by adding reverse osmosis (RO) water if necessary. In the period of rapid plant growth, soil moisture was adjusted twice daily. The removal of soil for analysis was considered when adjusting the water content.

Shoots of mature faba bean (*Vicia faba* L.) with C/N 60 were used as high C/N residue, shoots of young kikuyu grass (*Pennisetum clandestinum* L.) with C/N 20 as low C/N residue (Tab. 1). After collection, the shoots were oven dried at 40 °C, ground and sieved to particle size 0.25 - 2 mm. Residues added to pre-incubated soil at a total residue addition rate of 20 g kg^{-1}.

At the start of the experiment, either high (H) or low C/N residue (L) was added (Tab. 2). In treatments where only one residue type was added (H0, H7, H14, H21, H28, L0, L7, L14, L21 and L28) 20 g kg^{-1} of H or L residue was added on day 0. In HL0, a 1:1 mixture of H and L was added on day 0.

Tab. 1: Properties of low C/N (young kikuyu grass shoots) and high C/N (mature faba bean shoots) residues (n=3 ± standard error).

	Low C/N	High C/N
Total organic C (g kg^{-1})	$361^{\pm 5}$	$372^{\pm 3}$
Total N (g kg^{-1})	$17.7^{\pm 0.4}$	$6.3^{\pm 0.1}$
Total P (g kg^{-1})	$3.7^{\pm 0.1}$	$0.2^{\pm 0.0}$
C/N ratio	$20^{\pm 1}$	$60^{\pm 1}$
C/P ratio	$97^{\pm 4}$	$1585^{\pm 87}$

Tab. 2: Treatments and plant growth period, where H represents high C/N ratio residue and L low C/N residues. Shaded areas indicate plant growth period.

Period (days)		0-7	8-14	15-21	22-28	29-35	36-42	43-49
Treatment	Group*							
H7	Rd7	H						
H14	Rd14	H						
H21	Rd21	H						
H28	Rd28	H						
HL7	Rd7	H	L					
HL14	Rd14	H		L				
HL21	Rd21	H			L			
HL28	Rd28	H				L		
L7	Rd7	L						
L14	Rd14	L						
L21	Rd21	L						
L28	Rd28	L						
LH7	Rd7	L	H					
LH14	Rd14	L		H				
LH21	Rd21	L			H			
LH28	Rd28	L				H		

*Group names are based on the day on which the second residue was added.

In the HL or LH treatments, the combination of letters indicates the order in which the residues were added, i.e. H then L or L then H. In these treatments, 10 g kg^{-1} residue was added on day 0 and 10 g kg^{-1} of residue with the other C/N ratio was added on based on the day on which the second residue was added, i.e. Rd7, Rd14, Rd21 and Rd28 when the second residue was added on days 7, 14, 21 and 28. In Rd0, the second residue was added two hours after the first. At each addition, the residues were thoroughly mixed into the soil. After addition of the second residue, pre-germinated wheat seeds (*Triticum aestivum* L. cv Krichauff) were planted in all treatments of the group (H, L, HL and LH) and thinned to four plants per pot after three days. Pots were kept in a glasshouse with natural light in randomized block design and watered regularly by weight. During plant growth in Rd0 and Rd7, temperatures in the glasshouse exceeded 35 °C during the day. Although the pots were watered twice a day, the soil dried out between watering events. In the other treatment groups temperatures were lower and the soil water content could be maintained. In all treatments, the plants were harvested 28 days after planting.

Except for Rd0, available N and P were determined every seven days between the first and second residue addition and at plant harvest. On sampling days where residue application coincided with soil sampling, e.g. day 7 in H7 or L7, soil was sampled approximately three hours after residue addition. For a given treatment, the last soil sampling was conducted on the day the plants were harvested, 28 days after planting.

Soil texture was determined using the hydrometer method (Bowman et al., 2002). Soil maximum water holding capacity was measured using a sintered glass funnel (Haines, 1930). Soil pH and EC were measured in a 1:5 (w/v) soil to reverse osmosis (RO) water ratio after 1 h end-over-end shaking. Total organic carbon of soil and plant residues was determined after (Walkley and Black, 1934). Available N was extracted in 2 M KCl. Nitrate-N was measured in the filtered extract as described in Miranda et al. (2001), NH_4-N was determined according to Willis et al. (1996). Available N is the sum of NO_3-N and NH_4-N. Available P was determined by the anion exchange method of Kouno et al. (1995).

At harvest, plants were separated into shoots and roots which were washed and then dried at 65 °C. For total N and P in soil and shoots, the material was digested with H_2SO_4 and a mixture of HNO_3 and $HClO_4$, respectively. Total N was measured by a modified Kjeldahl method (Vanlauwe et al., 1996b). Total P in the digest was measured by the phosphovanado-molybdate method according to (Hanson, 1950). Shoot N and P uptake per pot was calculated by multiplying N and P concentration by shoot dry weight. Shoot N and P uptake per g

root was calculated as mg shoot N or P uptake divided by g root dry weight.

Statistical analysis

The experiment was arranged in a randomized block design with four replicates per treatment. Data was tested for normality and all data was normally distributed. Data of available N, P and pH was analysed by one-way repeated measures ANOVA for each group separately. When the interaction between treatment and sampling time was significant, post-hoc Tukey test was carried out on the treatment × sampling time interaction ($P \leq 0.05$). Additionally, soil data for a given sampling day was compared by one-way ANOVA across treatment groups. Plant data (root, shoot weight, shoot/root ratio, shoot N and P concentration etc.) was analysed by one-way ANOVA followed by Tukey test.

Results

Available N and P

In treatments where high C/N residue (H) was added at 20 g kg^{-1} on day 0 (H0, H7, H14, H21 and H28), available N was low and did not change over time (Fig. 1). However, it changed in the other treatments. In Rd0 (residues added and wheat planted on day 0), available N after residue addition and at harvest of wheat (day 28) in L0 and HL0 (20 g kg^{-1} as only L or 1:1 mixture of H and L) was ten-fold higher in L0 and four-fold higher in HL0 than in H0 (Fig. 1a).

In treatment group Rd7 (second residue added and wheat planted on day 7, harvest of wheat on day 35), available N at harvest was highest in L7 and lowest in H7 (Fig. 1b). It did not differ between HL7 and LH7 where it was about 50% lower than in L7. Available N decreased over time in treatments with L.

When the second residue added and wheat planted on day 14 (harvest of wheat on day 42, treatment group Rd14), changes in available N over time differed between L14, LH14 and HL14 (Fig. 1c). In L14, which had higher available N than the other treatments on day 14 and at harvest, available N increased from day 7 to day 14 about two-fold, but then decreased by 75% to harvest. In HL14, changes in available N over time were similar as in L14, but at a much lower level (about 50% lower). In LH14, available N was highest on day 7 and decreased over time.

In treatment group Rd21 (second residue added and wheat planted on day 21, harvest of wheat on day 49), available N did not change between days 7 and 14 and was about 5-fold greater in L21 and LH21 than in H21 and HL21 (Fig. 1d). On day 21 (after addition of the second residue in HL and LH) available N more than two-fold in L21 and eight-fold in HL21 than on day 14, but then decreased again to harvest by about 50%. In LH21, available N decreased from day 14 to harvest.

In treatment group Rd28 (second residue added and wheat planted on day 28, harvest of wheat on day 56), available N did not differ between days 7, 14 and 21 and was higher in L28 and LH28 than in H28 and HL28 (Fig. 1e). Compared to day 21, available N on day 28 (i.e. after the second residue addition in HL and LH) was two-fold higher in L28 and four-fold higher in HL28, but then decreased again to harvest with a greater relative decrease in LH28 than in L28 (by 30% compared to 10%). In LH28, available N decreased by about 50% from day 21 to day 28, but then remained unchanged until harvest.

In all treatments and groups, available P was highest at harvest (Fig. 2). In Rd0, available P n increased about five-fold from day 0 to harvest and was highest in L0 and lowest in H0 (Fig. 2a). At harvest, but not on day 0, available P was higher in HL0 than H0.

In all other treatment groups, available P did not differ among treatments on day 7 (Fig. 2). In Rd7 at harvest, when available P was up to 10-fold higher than on day 7, it was two-fold higher in L7, HL7 and LH7 than in H7 (Fig. 2b).

In Rd14, available P on day 14 (after the second residue addition in HL and LH) compared to day 7 was four-fold higher in L14, three-fold higher in HL14 and two-fold higher in LH14 (Fig. 2c). On day 14 and at harvest available P was highest in L14 and lowest in H14. Available P was similar in HL and LH and about 30% lower than in L14.

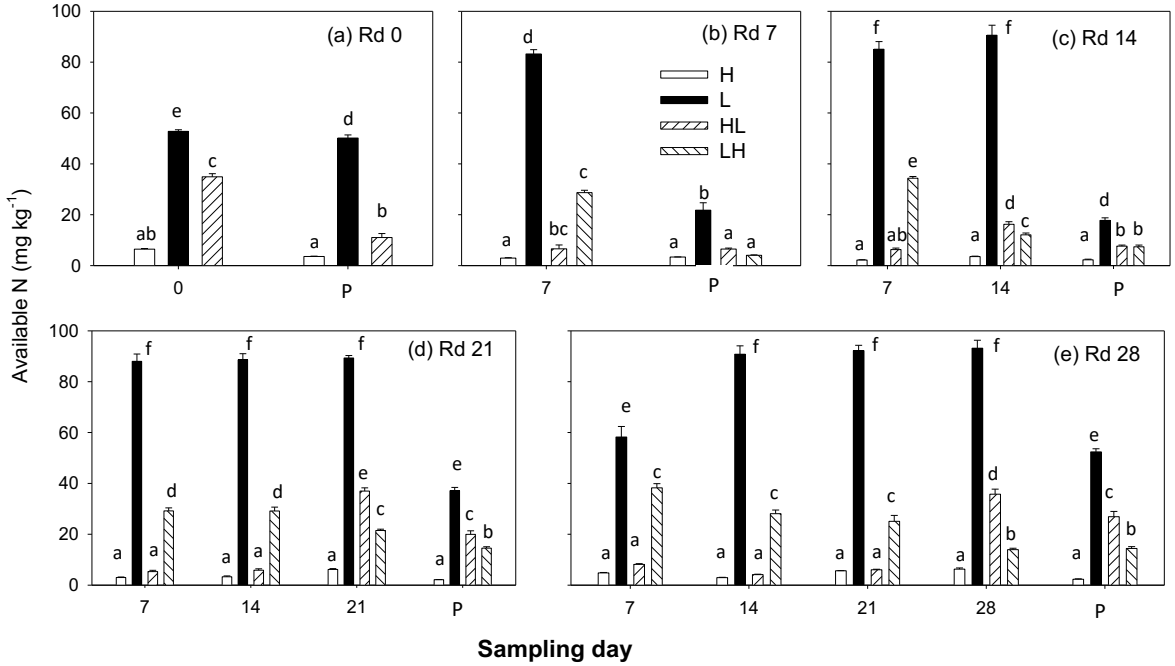

Fig. 1: Available N concentration on days 7, 14, 21, 28 and at plant harvest 28 days after planting (indicated by P) in treatments with only high C/N residue added (H), only low C/N residue added (L), high followed by low C/N (HL) or low followed by high (LH) where the second residue was added the same day as the first (a) or 7 (b), 14 (c), 21 (d) or 28 (e) days after the first (Rd0, Rd7, Rd14, Rd21, Rd28) 7 (a), 14 (b), 21 (c) or 28 (d) days after the first (Rd7, Rd14, Rd21, Rd28) (n=4 ± standard error). Columns within a treatment group with different letters are significantly different ($P \leq 0.05$).

Available P in Rd 21 was generally highest in L21 and lowest in H21 (Fig. 2d). On day 14, it was about 50% lower in HL21 than LH21, but after the second residue addition in HL and LH on day 21, later available P differed little between the two treatments where it was at least two-fold higher than in H21.

In Rd28, available P form day 14 was highest in L28 (Fig. 2e). On day 14, available P was lower in HL28 than in LH28, but the reverse was true on day 28 (after addition of the second residue) and at harvest. In HL28 and LH28 available P was about 30% lower than L28 and two-fold higher than in H28.

The soil pH ranged between 6 and 6.8 and changed little over time (data not shown). It tended to be highest after addition of H and lowest after L amendment.

Wheat growth and nutrient uptake

Treatment differences were more pronounced in shoot dry weight than total plant dry weight (Tab. 3). Shoot dry weight was always lowest with only H added and highest with only L added. Compared to the treatment with only L added, shoot dry weight was 20-30% lower in the two treatments with both L and H added (LH and HL). Shoot dry weight was similar in HL and LH, except for Rd28 where it was higher in LH28 than HL28.

Root dry weight did not differ among treatments in Rd0, Rd7 and Rd14 (Tab. 3). But in Rd21 and Rd28, root dry weight was lower in treatments with only H and L than in HL and LH.

Total plant dry weight was lowest in the treatments with only H added and highest with only L added (Tab. 3). It was similar in LH and

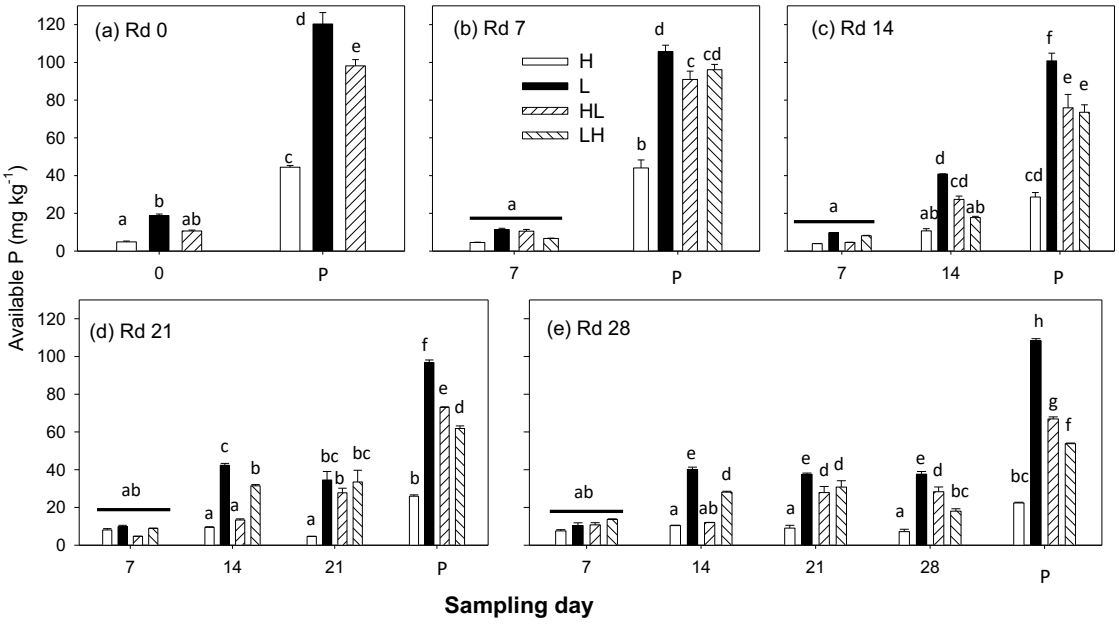

Fig. 2: Available P concentration on days 7, 14, 21, 28 and at plant harvest (indicated by P) in treatments with only high C/N residue added (H), only low C/N residue added (L), high followed by low C/N (HL) or low followed by high (LH) where the second residue was added the same day as the first (a) or 7 (b), 14 (c), 21 (d) or 28 (e) days after the first (Rd0, Rd7, Rd14, Rd21, Rd28) (n=4 ± standard error).
Columns within a treatment group with different letters are significantly different (P≤ 0.05).

Tab. 3: Shoot, root and total dry weight (g pot^{-1}) of wheat 28 days after the second residue addition in treatments with only high C/N residue added (H), only low C/N residue added (L), high followed by low C/N (HL) or low followed by high (LH) where the second residue was added 7, 14, 21 or 28 days after the first (Rd7, Rd14, Rd21, Rd28) (n=4 ± standard error). Values followed by different letters are significantly different (P≤ 0.05).

		Shoot			Root			Total			Shoot/root ratio		
		Dry weight (g pot^{-1})											
Rd7	H7	0.09	±0.01	a	0.17	±0.01	abcd	0.25	±0.02	a	0.51	±0.04	a
	L7	0.52	±0.01	gh	0.20	±0.01	abcde	0.71	±0.02	fg	2.66	±0.14	h
	HL7	0.30	±0.02	b	0.20	±0.02	bcde	0.50	±0.04	cd	1.52	±0.07	cde
	LH7	0.29	±0.02	b	0.21	±0.02	bcde	0.49	±0.04	bc	1.41	±0.07	cd
Rd14	H14	0.21	±0.10	a	0.15	±0.01	abc	0.36	±0.11	a	1.38	±0.63	ab
	L14	0.44	±0.11	efg	0.13	±0.04	abcde	0.57	±0.16	fg	2.63	±0.69	i
	HL14	0.45	±0.03	efg	0.19	±0.01	abcde	0.63	±0.04	cdefg	2.38	±0.08	h
	LH14	0.43	±0.03	ef	0.21	±0.02	bcde	0.64	±0.05	cdefg	2.09	±0.11	fgh
Rd21	H21	0.10	±0.01	a	0.13	±0.01	a	0.23	±0.01	a	0.79	±0.06	ab
	L21	0.64	±0.01	i	0.14	±0.00	ab	0.78	±0.01	g	4.47	±0.18	j
	HL21	0.50	±0.02	gh	0.22	±0.02	cde	0.72	±0.04	fg	2.31	±0.11	gh
	LH21	0.47	±0.01	fgh	0.24	±0.02	e	0.71	±0.02	fg	2.00	±0.14	fgh
Rd28	H28	0.10	±0.01	a	0.15	±0.01	abc	0.25	±0.02	a	0.67	±0.02	ab
	L28	0.50	±0.05	gh	0.16	±0.02	abcd	0.66	±0.06	defg	3.25	±0.10	i
	HL28	0.37	±0.01	cde	0.22	±0.01	de	0.59	±0.01	cdef	1.67	±0.09	def
	LH28	0.45	±0.01	efg	0.24	±0.01	e	0.69	±0.02	defg	1.91	±0.09	efg

Tab. 4: Shoot and root N and P concentration (g kg^{-1}) and uptake (mg pot^{-1}) of wheat 28 days after the second residue addition in treatments with only high C/N residue added (H), only low C/N residue added (L), high followed by low C/N (HL) or low followed by high (LH) where the second residue was added 7, 14, 21 or 28 days after the first (Rd7, Rd14, Rd21, Rd28) (n=4 ± standard error). Values followed by different letters are significantly different (P≤ 0.05).

		Shoot											
		N concentration			P concentration			N uptake			P uptake		
Group	Treatment	g N kg^{-1}			mg P kg^{-1}			mg N pot^{-1}			mg P pot^{-1}		
Rd7	H7	19.11	±2.62	b	3.50	±0.16	b	1.56	±0.10	a	0.30	±0.03	a
	L7	33.18	±1.08	efgh	6.12	±0.15	h	17.07	±0.62	f	3.15	±0.06	h
	HL7	34.66	±1.40	fgh	5.28	±0.28	efgh	10.40	±0.49	cd	1.59	±0.11	bcde
	LH7	31.57	±2.41	efgh	4.70	±0.33	cdefg	8.84	±0.23	bcd	1.32	±0.06	bc
Rd14	H14	21.97	±1.84	ab	4.22	±0.52	bc	5.24	±3.02	a	1.05	±0.65	a
	L14	20.13	±6.11	bcde	4.22	±1.25	fgh	11.69	±2.89	ef	2.44	±0.61	gh
	HL14	28.09	±2.36	efgh	4.37	±0.26	bcde	12.30	±0.15	de	1.92	±0.03	cdef
	LH14	27.62	±1.91	cdef	3.98	±0.12	bcd	11.76	±0.15	de	1.71	±0.09	cdef
Rd21	H21	21.82	±0.26	bcd	3.84	±0.08	bcd	2.18	±0.14	a	0.38	±0.03	a
	L21	36.16	±0.21	h	4.94	±0.11	defg	22.96	±0.36	g	3.13	±0.05	h
	HL21	35.46	±0.57	gh	4.17	±0.24	bcde	17.81	±0.75	f	2.08	±0.06	def
	LH21	31.62	±1.02	efgh	3.63	±0.15	bc	14.78	±0.58	ef	1.69	±0.05	cdef
Rd28	H28	22.90	±0.55	bcd	2.25	±0.07	a	2.29	±0.16	a	0.22	±0.02	a
	L28	33.94	±1.41	efgh	4.59	±0.44	bcdefg	17.15	±2.05	f	2.37	±0.48	fg
	HL28	30.69	±1.23	efgh	3.84	±0.15	bcd	11.38	±0.70	de	1.43	±0.09	bcd
	LH28	35.21	±1.21	fgh	4.18	±0.31	bcde	15.84	±0.62	f	1.88	±0.14	cdef

Tab. 5: Shoot N and P uptake per g root of wheat 28 days after the second residue addition in treatments with only high C/N residue added (H), only low C/N residue added (L), high followed by low C/N (HL) or low followed by high (LH) where the second residue was added 7, 14, 21 or 28 days after the first (Rd7, Rd14, Rd21, Rd28) or full residue amount added on day 0 (Rd0)(n=4 ± standard error). Values followed by different letters are significantly different (P≤ 0.05).

Group	Treatment	N uptake			P uptake		
		mg pot^{-1}					
Rd0	H0	4.96	±0.30	a	1.83	±0.17	ab
	L0	43.37	±4.06	bc	12.54	±0.48	fg
	HL0	39.83	±0.66	b	5.51	±0.26	bcd
Rd7	H7	9.59	±0.94	a	1.78	±0.10	ab
	L7	87.99	±2.91	f	16.32	±1.09	gh
	HL7	52.52	±2.81	bcd	8.02	±0.63	de
	LH7	44.68	±4.78	bc	6.66	±0.69	cde
Rd14	H14	15.70	±1.09	a	2.83	±0.11	abc
	L14	87.29	±4.58	f	18.28	±1.57	hi
	HL14	66.60	±5.10	de	10.37	±0.58	ef
	LH14	57.92	±6.27	bcd	8.34	±0.65	de
Rd21	H21	17.25	±1.10	a	3.03	±0.19	abc
	L21	161.75	±6.76	h	22.07	±0.84	i
	HL21	81.99	±4.21	ef	9.72	±0.95	ef
	LH21	63.51	±6.19	cde	7.28	±0.71	de
Rd28	H28	15.40	±0.64	a	1.51	±0.07	a
	L28	110.12	±3.26	g	14.91	±1.41	gh
	HL28	51.60	±4.76	bcd	6.44	±0.52	cde
	LH28	66.99	±1.81	de	8.04	±0.92	de

HL and about two-fold than with H only. Total plant dry weight in HL and LH was about 25% lower than L in Rd0 and Rd7, but did not differ among these treatments when the second residue was added 14 or more days after the first (Rd14, Rd21 and Rd28).

The shoot/root dry weight ratio was lowest when only H residue was added and highest with only L residue (Tab. 3). In HL and LH, the ratio was lower than with only L added, but more than twice as high than with only H amendment.

The shoot N and P concentration with only H residue added was about 30% lower than in the other treatments (Tab. 4). Shoot N concentration was similar in treatments with L residue (L, HL and LH), except in Rd0 where it was higher in the mixed treatments than with only L added. Shoot P concentration did not differ among treatments with L addition (L, HL and LH), except in Rd14 and Rd21 where it was about 25% lower in HL and LH than in L.

Shoot N and P uptake (mg pot^{-1}) was lowest with only H amendment where it was four to six-fold lower than in the treatments with L added (L, LH and HL) (Tab. 4). Shoot N uptake was about 25% lower in HL and LH than in L except in Rd0 and Rd14 where it did not differ among treatments with L. Shoot P uptake was 30-50% lower in HL and LH than in L, the only exception was Rd28 where shoot P uptake did not differ between L and LH. Shoot N and P uptake per g root was about five-fold lower when only H was added compared to treatments amended with L (Tab. 5). Shoot N uptake per g root was highest with only L amendment where it was 25-30% higher than in HL and LH which did not differ in shoot N uptake per g root. Compared to HL and LH, shoot P uptake per g root was 0.3 to two-fold higher with only L amendment.

Discussion

This study confirmed the existence of a legacy effect of the previous residue addition on nutrient availability after the second addition (Marschner et al., 2015; Nguyen et al., 2016), but also showed that in treatments where both low and high C/N residues are present (HL and LH) plants compensate lower N and P availability compared to L only by developing a more extensive root system.

Available N and P

The first hypothesis (N and P availability after the second residue are influenced by the legacy effect, i.e., is lower when low C/N residue follows high C/N residue than if low C/N residue follows low C/N residue) can be confirmed.

Before the second residue addition, available N and P were as expected from many previous studies (KWABIAH et al., 2003; TIAN et al., 1992a). They followed the order H=HL < LH=L. Immediately after the second residue addition (days 7, 14, 21 and 28 in Rd7, Rd14, Rd21 and Rd28, respectively), available N and P were influenced by the legacy effect because they were affected by both C/N ratio of the second residue and the C/N ratio of the previously added residue. They were in the order H < LH < HL < L. Thus in LH, presence of L in soil when H was added increased available N and P compared to H whereas addition of L into a soil containing H (HL) reduced nutrient availability compared to L. But at harvest of wheat (28 days later), differences in available N and P between HL and LH were smaller or there were no differences between the two treatments. In previous studies, we also found that differences in available N and P between HL and LH decreased with time after the second residue addition (MARSCHNER et al., 2015; NGUYEN et al., 2016). This can be explained by decreasing residue decomposition rates due to depletion of easily decomposable compounds (MARSCHNER et al., 2014; WESSELS PERELO and MUNCH, 2005), and in this study, plant N and P uptake. Compared to immediately after the second residue addition, available N was lower at harvest, which indicates that plant N uptake exceeded N net mineralisation. In contrast, available P was higher at harvest than immediately after the second residue addition, suggesting than P mineralisation was greater than P uptake, probably because root density was not very high and P is poorly mobile in soil (e.g. BERTRAND et al., 2003).

The lower pH in soil amended with L compared to H residue is likely due to greater nitrification with the former due to its higher N concentration (XU et al., 2006).

The second hypothesis (the legacy effect on N and P availability will decrease with time between residue additions) can be confirmed for available N, but not for available P. N availability did not differ between HL and LH when the second residue was added seven days after the first (Rd7) and the differences were smaller when there were 14 days between first and second addition (Rd14) than in treatments where the second residue was added 21 or 28 days after the first (Rd21, Rd28). The lack of difference between HL and LH when there were two weeks or less between residue additions may be because relatively large amounts of the previously added residue was still in the soil when the second residue was added. With longer time between residue additions, the amount of the previously added residue would be low and nutrient availability mainly affected by the second residue added. There was no clear pattern in available P immediately after the second residue addition with time between residue additions. Available P did not differ among treatments in Rd7 and Rd21, but in Rd14 and Rd28, the available P concentration was greater in HL than in LH.

Wheat growth and nutrient uptake

Plant growth in Rd0 and Rd7 was lower compared to the other treatment groups. This is likely to be due to the much higher temperature in the glasshouse during this time (> 35 °C during the day) compared to the other treatment groups (20 - 25 °C during the day). This temperature difference may have confounded any effect of time between residue additions on plant growth. To minimise this environmental effect in future experiments, plant growth should occur in all treatments at the same time.

When only H was added, shoot and total plant dry weight as well as shoot N and P concentrations were low compared to the other treatments which can be explained by the low soil available N and P concentrations. Shoot dry weight in H was about five-fold lower than in L and the shoot/root dry weight ratio was also lower in H. Thus the plants responded to the low nutrient availability in H by a growing a more extensive root system, which is a common response in plants to the low nutrient availability (MARSCHNER, 2012). However, even with the greater root system, shoot and total plant growth and shoot N and P concentrations were lower in H than in the other treatments. Wheat in the treatment with only L added had the highest shoot and total dry weight and up to two-fold higher shoot N and P concentrations than plants with only H added which can be explained by the greater available N and P concentrations in the former. Since root dry weight did not differ between the two treatments, the shoot/root ratio was lower in L than in H. A relatively small root system compared to the shoots is a common plant response to high nutrient availability (MARSCHNER, 2012).

Shoot N concentrations were higher in LH than in H, which can be explained by the higher soil N availability in the former. However, shoot N concentrations did not differ between HL and L although N availability was lower in the former. However, HL had a lower shoot/root ratio than L. Thus relative to the shoots, plants in HL had more roots than those in L which allowed them to take up more N than would be expected based on available N concentrations.

The third hypothesis (plant growth and N and P concentrations after the second residue will be influenced by the legacy effect, i.e., will be greater if high C/N residue follows low C/N residue than if high C/N residue follows high C/N residue, and will be greater with low following high C/N residue than with high following low C/N residue) can only be partly confirmed. Plant growth and shoot N and P concentrations after the second residue addition were influenced by the legacy effect, i.e., were greater if high C/N residue followed low C/N residue (LH) than only high C/N residue was added. However, plant growth and N and P concentrations did not differ between HL and LH. It was expected that plant growth and shoot N and P concentrations would be lower in LH the HL because available N and P concentrations immediately after the second residue addition were lower in the former. However, there were no differences in shoot, root dry weight or shoot N and P concentrations between the two treatments. This indicates that the plants were able to compensate differences in available N and P concentrations in the soil by an extensive root system.

Time between the first and second residue influenced soil N availability, but not the differences in total plant dry weight between L and HL or HL and LH. This too indicates that wheat compensated lower nutrient availability by growing more roots.

Conclusion

The study showed that plants can compensate for legacy-induced differences in nutrient availability by a larger root system. This larger root system also over-rode the effect of time between residue additions on soil nutrient availability. Thus the impact of the legacy effect on crop growth may be smaller than expected from soil nutrient availability. This indicates for plants with an extensive root system, the order in which H and L are added and the time between residue additions is not important. However, in soils where root growth is restricted or in plants with inherently small root systems, the influence of the legacy effect on plant growth may be greater.

Conflict of interest

The authors confirm that there is no potential conflict of interest.

References

BERTRAND, I., HOLLOWAY, R.E., ARMSTRONG, R.D., MCLAUGHLIN, M.J., 2003: Chemical characteristics of phosphorus in alkaline soils from southern Australia. Aust. J. Soil Res. 41, 61-76. DOI: 10.1071/SR02021

BOWMAN, G., HUTKA, J., MCKENZIE, N., COUGHLAN, K., CRESSWELL, H., 2002: Particle size analysis. Soil physical measurement and interpretation for land evaluation. CSIRO Publishing.

Carrillo, Y., Ball, B.A., Strickland, M.S., Bradford, M.A., 2012: Legacies of plant litter on carbon and nitrogen dynamics and the role of the soil community. Pedobiologia 55, 185-192. DOI: 10.1016/j.pedobi.2012.02.002

Conyers, M.K., Moody, P.W., 2009: A conceptual framework for improving the P efficiency of organic farming without inputs of soluble P fertiliser. Crop Pasture Sci. 60, 100-104. DOI: 10.1071/cp06327

Cordell, D., Drangert, J., White, S., 2009: The story of phosphorus: global food security and food for thought. Glob. Environ. Change 19, 292-305. DOI: 10.1016/j.gloenvcha.2008.10.009

Enwezor, W.O., 1976: Mineralization of nittogen and phosphorus in organic materials of varying C-N and C-P ratios. Plant Soil 44, 237-240. DOI: 10.1007/bf00016972

Flavel, T.C., Murphy, D.V., 2006: Carbon and nitrogen mineralization rates after application of organic amendments to soil. J. Environ. Qual. 35, 183-193. DOI: 10.2134/jeq2005.0022

Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012: Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. J. Ecol. 100, 619-630. DOI: 10.1111/j.1365-2745.2011.01943.x

Hadas, A., Kautsky, L., Goek, M., Kara, E.E., 2004: Rates of decomposition of plant residues and available nitrogen in soil, related to residue composition through simulation of carbon and nitrogen turnover. Soil Biol. Biochem. 36, 255-266. DOI: 10.1016/j.soilbio.2003.09.012

Haines, W.B., 1930: Studies in the physical properties of soil. V. The hysteresis effect in capillary properties, and the modes of moisture distribution associated therewith. J. Agric. Sci. 20, 97-116.

Hanson, W.C., 1950: The photometric determination of phosphorus in fertilizers using the phosphovanado-molybdate complex. J. Sci. Food. Agric. 1, 172-173. DOI: 10.1002/jsfa.2740010604

Hargreaves, J.C., Adl, M.S., Warman, P.R., 2008: A review of the use of composted municipal solid waste in agriculture. Agric. Ecosyst. Environ. 123. DOI: 10.1016/j.agee.2007.07.004

Isbell, R., 2002: The Australian Soil Classification. CSIRO Publishing.

Kouno, K., Tuchiya, Y., Ando, T., 1995: Measurement of soil microbial biomass phosphorus by an anion exchange membrane method. Soil Biol. Biochem. 27, 1353-1357. DOI: 10.1016/0038-0717(95)00057-L

Kwabiah, A.B., Palm, C.A., Stoskopf, N.C., Voroney, R.P., 2003: Response of soil microbial biomass dynamics to quality of plant materials with emphasis on P availability. Soil Biol. Biochem. 35, 207-216. DOI: 10.1016/S0038-0717(02)00253-5

Lewis, D.B., Kaye, J.P., Kinzig, A.P., 2014: Legacies of agriculture and urbanization in labile and stable organic carbon and nitrogen in Sonoran Desert soils. Ecosphere 5, 59. DOI: 10.1890/es13-00400.1

Marschner, P., 2012: Marschner's Mineral Nutrition of Higher Plants. Elsevier, London.

Marschner, P., Hatam, Z., Cavagnaro, T.R., 2014: Soil respiration, microbial biomass and nutrient availability after the second amendment are influenced by legacy effects of prior residue addition. Soil Biol. Biochem. 88, 169-177. DOI: 10.1016/j.soilbio.2015.05.023

Marschner, P., Hatam, Z., Cavagnaro, T.R., 2015: Soil respiration, microbial biomass and nutrient availability after the second amendment are influenced by legacy effects of prior residue addition. Soil Biol. Biochem. 88, 169-177. DOI: 10.1016/j.soilbio.2015.05.023

Miranda, K.M., Espey, M.G., Wink, D.A., 2001: A rapid, simple spectrophotometric method for simultaneous determination of nitrate and nitrite. Nitric oxide 5, 62-71. DOI: 10.1006/niox.2000.0319

Nguyen, T.T., Cavagnaro, T.R., Ngo, H.T.T., Marschner, P., 2016: Soil respiration, microbial biomass and nutrient availability in soil amended with high and low C/N residue – influence of interval between residue additions. Soil Biol. Biochem. 95, 189-197. DOI: 10.1016/j.soilbio.2015.12.020

Nwoke, O.C., Vanlauwe, B., Diels, J., Sangina, N., Osonubi, O., 2004: Impact of residue characteristics on phosphorus avaialbility in West African moist savanna soils. Biol. Fertil. Soils 39, 422-428. DOI: 10.1007/s00374-004-0731-9

Quilty, J.R., Cattle, S.R., 2011: Use and understanding of organic amendments in Australian agriculture: a review. Soil Res. 49, 1-26, DOI: 10.1071/SR10059

Rashid, M.I., de Goede, R.G.M., Brussaard, L., Lantinga, E.A., 2013: Home field advantage of cattle manure decomposition affects the apparent nitrogen recovery in production grasslands. Soil Biol. Biochem. 57, 320-326. DOI: 10.1016/j.soilbio.2012.10.005

Staff, S.S., 2014: Keys to Soil Taxonomy. USDA-Natural Resources Conservation Service, Washington, DC.

Strickland, M.S., Osburn, E., Lauber, C., Fierer, N., Bradford, M.A., 2009: Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Funct. Ecol. 23, 627-636. DOI: 10.1111/j.1365-2435.2008.01515.x

Tian, G., Kang, B.T., Brussaard, L., 1992a: Biological effects of plant residues with contrasting chemical composiitons under humid tropical conditions – decomposition and nutrient release. Soil Biol. Biochem. 24, 1051-1060. DOI: 10.1016/0038-0717(92)90035-v

Tian, G., Kang, B.T., Brussaard, L., 1992b: Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions – decomposition and nutrient release. Soil Biol. Biochem. 24, 1051-1060. DOI: 10.1016/0038-0717(92)90035-v

Vanlauwe, B., Nwoke, O.C., Sanginga, N., Merckx, R., 1996a: Impact of residue quality on the C and N mineralization of leaf and root residues of three agroforestry species. Plant Soil 183, 221-231. DOI: 10.1007/bf00011437

Vanlauwe, B., Nwoke, O.C., Sanginga, N., Merckx, R., 1996b: Impact of residue quality on the C and N mineralization of leaf and root residues of three agroforestry species. Plant Soil 183, 221-231. DOI: 10.1007/BF00011437

Walkley, A., Black, I.A., 1934: An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 37, 29-38.

Wessels Perelo, L., Munch, J.C., 2005: Microbial immobilisation and turnover of 13C labelled substrates in two arable soils under field and laboratory conditions. Soil Biol. Biochem. 37, 2263-2272. DOI: 10.1016/j.soilbio.2005.02.039

Willis, R.B., Montgomery, M.E., Allen, P.R., 1996: Improved method for manual, colorimetric determination of total Kjeldahl nitrogen using salicylate. J. Agricult. Food Chem. 44, 1804-1807. DOI: 10.1021/jf950522b

Xu, J.M., Tang, C., Chen, Z.L., 2006: The role of plant residues in pH change of acid soils differing in initial pH. Soil Biol. Biochem. 38, 709-719. DOI: 10.1016/j.soilbio.2005.06.022

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