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Winter cover crop legacy effects on litter decomposition act through litter quality and microbial community changes

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Abstract

1. In agriculture, winter cover crop (WCC) residues are incorporated into the soil to improve soil quality, as gradual litter decomposition can improve fertility. Decomposition rate is determined by litter quality, local soil abiotic and biotic properties. How these factors are interlinked and influenced by cropping history is, however, unclear.
2. We grew WCC monocultures and mixtures in rotation with main crops *Avena sativa* (oat) and *Cichorium endivia* (endive) and tested how crop rotation influences WCC litter quality, abiotic and biotic soil conditions, and litter decomposition rates. To disentangle WCC litter quality effects from WCC soil legacy effects on decomposition, we tested how rotation history influences decomposition of standard substrates and explored the underlying mechanisms.
3. In a common environment (e.g. winter fallow plots), WCC decomposition rate constants (*k*) correlated negatively with litter C, lignin and, surprisingly, N content, due to strong positive correlations among these traits. Plots with a history of fast-decomposing WCCs exhibited faster decomposition of their own litters as well as of the standard substrates filter paper and rooibos tea, as compared to winter fallow plots.
4. WCC treatments differentially affected soil microbial biomass, as well as soil organic matter and mineral nitrogen content. WCC-induced soil changes affected decomposition rates. Depending on the main crop rotation treatment, legacy effects were attributed to biomass input of WCCs and their litter quality or changes in microbial biomass.
5. *Synthesis and applications.* These results demonstrate that decomposition in cropping systems is influenced directly through crop residues, as well as through crop-induced changes in soil biotic properties. Rotation history influences decomposition, wherein productive winter cover crops (WCC) with low lignin content decompose fast and stimulate the turnover of both own and newly added residues via their knock-on effect on the soil microbial community. Thus, WCC have promise for sustainable carbon- and nutrient-cycling management through litter feedbacks.

KEYWORDS
carbon cycling, crop rotation, decomposition, legacy effects, microbial community composition, nitrogen cycling, standardised substrates, winter cover crop

1 | INTRODUCTION

Decomposition of fresh organic matter initiates the cycling of newly added nitrogen (N) and carbon (C) in soils, which is fundamental to soil fertility. Litter quality, environmental conditions, decomposer biomass and community composition are major drivers of litter decomposition (Bradford, Berg, Maynard, Wieder, & Wood, 2016; Cornwell et al., 2008; Swift et al., 1979). Plants, in turn, shape several of these controlling factors, namely litter quality, abiotic soil properties and decomposer community composition (Hobbie, 2015; Van der Putten, Bradford, Brinkman, van de Voorde, & Veen, 2016; Veen, Freschet, Ordonez, & Wardle, 2015). However, our understanding of how plant legacies affect decomposition rates remains limited, despite benefits of such understanding to sustainable management of agroecosystems.

In agroecosystems, cover crop cultivation improves soil quality through incorporation of crop residues (Dias, Dukes, & Antunes, 2014). N-fixing legumes are grown as green manures, whereas grasses and deep-rooting Brassicaceae can catch mineral N vulnerable to leaching (Thorup-Kristensen, Magid, & Jensen, 2003). Subsequent crop productivity is stimulated by both quantity and quality of winter cover crops (WCCs), presumably via decomposition and mineralisation (Barel, Kuyper, de Boer, Douma, & de Deyn, 2018). Decomposition rates and associated nutrient release from plant litter relate to litter traits as decomposition is impeded by recalcitrant compounds such as lignin, and stimulated by high N concentrations (Cornwell et al., 2008; Freschet, Aerts, & Cornelissen, 2012b). Depending on litter quality, organic N can be mineralised or immobilised, thus changing mineral N availability for subsequent plant growth and ecosystem functioning via litter legacy effects (Hobbie, 2015; Parton et al., 2007).

Locally, decomposer community activity is regulated by a range of factors (Bradford et al., 2016). For example, mineral N can limit break-down of lignin by soil microbes in later stages of decomposition (Berg & Meentemeyer, 2002), while N availability stimulates decomposition of cellulose (Hu & van Bruggen, 1997). Mineral N availability, in turn, is influenced by plant growth history through nitrogen uptake and release, or through alterations of soil organic matter (SOM) content and pH (Barel, Kuyper, de Boer, et al., 2018; Duval, Galantini, Capurro, & Martinez, 2016; Vanzolini, Galantini, Martínez, & Suñer, 2017). Clearly plant legacies may affect abiotic soil conditions, thus influencing decomposition. Yet, these legacy effects are poorly understood.

Since saprotrophic microbes are the actors of decomposition, their abundance and functioning determine decomposition rates, on top of or in interaction with inherent litter quality (Strickland, Osburn, Lauber, Fierer, & Bradford, 2009; Wickings, Grandy, Reed, & Cleveland, 2012). For example, soil microbial communities with high fungal to bacterial (F:B) ratios break-down recalcitrant litter faster than communities with a low F:B (van der Wal, Geydan, Kuyper, & de Boer, 2013). Microbial communities can respond rapidly to the crops they are exposed to, as microbial biomass was found to increase and F:B ratio to decrease with increasing temporal crop diversity in crop rotations (Tiemann, Grandy, Atkinson, Marin-Spiotta, & McDaniel, 2015). Moreover, Gram-positive bacteria and microbial activity increased with inclusion of cover crops into rotations (Brennan & Acosta-Martinez, 2017; Chavarría et al., 2016). Thus, WCC could provide a means of managing decomposition processes in soil, directly through crop residue inputs as well as indirectly through changes in abiotic and biotic soil conditions. But it remains to be tested to what extent WCCs affect the decomposition process during the following cropping season.

Plant legacy effects on decomposition processes may be general in nature, or litter quality specific as has been shown in numerous studies in natural ecosystems. Repeated litter inputs can result in functional specialisation of the local decomposer community, which decomposes home litters faster than foreign litters: the so-called home-field advantage (HFA; Austin, Vivanco, González-Arzac, & Pérez, 2014; Ayres, Steltzer, Berg, & Wall, 2009; Keiser, Strickland, Fierer, & Bradford, 2011). Such litter affinity can also occur with introduced litters of similar quality as the home litter, wherein affinity decreases with increasing quality-contrast between the home and introduced litters (Freschet, Aerts, & Cornelissen, 2012a). Generally, recalcitrant litters benefit most from home-decomposer specialisation (Wallenstein et al., 2013). Agroecosystems, however, are typically subjected to high nutrient inputs, high-quality litters and frequent disturbance, possibly weakening local decomposer specialisation. Nevertheless, HFA was observed for locally produced cattle-manure (Rashid, de Goede, Brussaard, & Lantinga, 2013), and in potato cultivation (Brolsma, Vonk, Hoffland, Mulder, & de Goede, 2015). Thus, the question arises whether WCCs develop specific legacies, altering decomposition of own residues and newly added amendments. Alternatively, WCCs may increase the soils general ability to decompose organic matter regardless of its quality, by inducing a favourable soil environment. For example, legume presence in grassland systems can increase decomposition of contrasting substrates cellulose and wood (Scherer-Lorenzen, 2008). Closing the knowledge gap of plant legacy effects on drivers of decomposition in crop rotation would be an important contribution to soil fertility management.

In this study, we aimed to understand how crop rotation design influences decomposition of WCC litters through litter traits and via legacy effects on soil abiotic and biotic properties. First, we tested

(1) how crop rotation shaped WCC litter legacies. We predicted (1a) that high litter quality (high litter N- and low C- and lignin content) results in fast decomposition in a common environment. Also, we predicted (1b) that different crop rotations result in distinct soil abiotic conditions (soil organic matter, mineral N, potential mineralisation, pH), microbial biomass and community composition. Second, we tested (2) underlying mechanisms of litter legacy effects on decomposition. By comparing WCC litter decomposition in own plots with decomposition of four standard substrates, we tested (2a) whether the WCC legacy effects on decomposition were litter quality specific or general. Last, we tested (2b) the importance of WCC residue quantity and quality, soil abiotic and biotic conditions as drivers of WCC litter legacy effects.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Winter cover crop legacy on litter decomposition was tested in a field experiment on arable sandy soil at the field facilities of Wageningen University (Wageningen, The Netherlands, 51°59′41.9″N 5°39′17.5″E). A full description of the experimental design is given in Barel, Kuyper, de Boer, et al. (2018). Briefly, the set-up was as follows (see also Supporting Information Figure S1).

In spring 2014, monocultures of *Avena sativa* L. (oat) and *Cichorium endivia* L. (endive) were grown on 3 × 3 m plots and harvested in July. Six WCC treatments and fallow (as control) were established in August 2014. WCC treatments included monocultures of *Lolium perenne* L. (English ryegrass), *Trifolium repens* L. (white clover), *Vicia sativa* L. (common vetch), *Raphanus sativus* L. (fodder radish) (hereafter, referred to by their generic names) and mixtures (50:50 seeding density): *Lolium+Trifolium* (L+T), *Raphanus+Vicia* (R+V). In February 2015, WCCs were incorporated into the soil (0–10 cm) by rotary tilling. Fallow plots were treated similarly. In spring 2015, *Avena* and *Cichorium* were factorially cultivated as monocultures. This complete randomised block design included 28 rotations (2 × 7 × 2 treatments) replicated in five blocks.

Winter cover crop legacy effects on soil abiotic and biotic properties and on *in situ* litter decomposition was studied during the third growing season (April–June 2015).

2.2 | WCC litter quality, litterbag preparation and incubation

In the second week of December 2014, WCC litters were collected as fresh plant material cut at soil surface from a 25 × 25 cm area, dried (70°C) and weighed as shoot biomass (g dw/m^2) (presented in Barel, Kuyper, de Boer, et al. 2018). At time of collection *Vicia* plants were partially senesced. Litter C, N and lignin content were determined using standard protocols (as described in Barel, Kuyper, de Boer, et al. 2018 and Supporting Information).

Winter cover crop litterbags were prepared for incubation in own- and fallow-plots (2 × 120 litterbags, incl. five replications). Litterbags measured 5 × 5 cm of polyester fabric (0.02 mm mesh size). WCC litterbags contained 1 g dried litter cut to 1 cm length; *Trifolium* litterbags contained 0.75 g and were replicated three times due to limited litter availability. In addition, four contrasting standard substrates were incubated in all plots (4 × 140 litterbags, incl. five replications) namely: filter paper (Whatman GmbH, Dassel, Germany, ref. no. 10 311 645), bamboo satay-sticks (Vanka-Kawat, Den Haag, The Netherlands, article no. 87601) as simple lignin poor versus lignin rich substrates, green tea and rooibos tea (Lipton EAN:8722700055525 resp. EAN: 8722700188438) as complex substrates with different decomposition rates (Keuskamp, Dingemans, Lehtinen, Sarneel, & Hefting, 2013). Green tea and rooibos tea were prepared according to Keuskamp et al. (2013). Filter paper and bamboo sticks were cut to 2 cm and used to fill another series of unused emptied tea bags (mesh size 0.25 mm) with 2 g.

All litterbags were buried vertically at 8 cm depth, 20 cm apart, in early April and were retrieved after 63 days, stored at 4°C for maximally 1 week until cleaning. Litterbags were gently rinsed to remove adherent soil and roots, dried at 70°C and remaining litter was weighed after removal of ingrown roots.

2.3 | Soil abiotic and microbiological properties

Abiotic soil properties and microbial community composition were assessed in bulk soil samples taken at time of litterbag burial. Per plot, three auger cores (2.5 cm diameter, 0–30 cm) were taken for one composite sample (140 samples in total). Samples were stored (4°C, <1 week), sieved (2 mm) and split for the following analyses.

Soil organic matter, soil mineral nitrogen(NO3+NH4) and potential N mineralisation were quantified as described in Barel, Kuyper, de Boer, et al. (2018) (see also Supplements). Soil pH was measured in a 1:5 (w/v) suspension of dry soil in 1 M KCl. Soil volumetric moisture content and temperature were recorded by TMS-3 dataloggers (TOMST, Prague, Czech Republic), placed in fallow plots (see Supporting Information).

Microbial community composition was assessed by phospholipid fatty acid (PLFA) analysis of 3 g of sieved freeze-dried soil per plot, as described in Hedlund (2002). Twenty-seven PLFAs were detected and quantified (Supporting Information Table S5), of which i15:00, a15:00, i16:00, i17:00 and a17:00 were classified as gram-positive bacteria, cy17:00, 18:1ω7 and cy19:00 as gram-negative bacteria, and 15:00, 16:1ω9, 16:1ω7c and 17:00 as general bacterial markers (Frostegård & Bååth, 1996), and 18:2ω6 was used as indicator of saprotrophic-fungal biomass (Hedlund, 2002). Fungal and bacterial markers were used to calculate fungal to bacterial biomass ratio (F:B) (Frostegård & Bååth, 1996).

Fungal biomass was also estimated by ergosterol biomass, according to Bååth (2001) and de Ridder-Duine, Smant, van der Wal,

van Veen, and de Boer (2006) with minor protocol modifications (see Supporting Information).

2.4 | Data analysis

Data were analysed with R statistical software version 3.3.1 (R Core Team, 2016) using the below-mentioned packages.

For all litters and substrates exponential mass loss was assumed. Decomposition rate k (day^{-1}) was calculated according to Olson (1963): the fraction remaining mass (f_{rem}) was modelled as a function of incubation duration (t [days]):

$$f_{rem} = e^{-kt}$$

Differences in litter quality between WCC species and their preceding main crops (Hypothesis 1a) were tested with separate mixed effects models for response variables litter N-, C- and lignin concentration (nlme package; Pinheiro, Bates, DebRoy, & Sarkar, 2016), following the protocol by Zuur, Ieno, Walker, Saveliev, and Smith (2010). Full models included main effects and interaction between WCC species and preceding main crop treatment (WCC*S14). Block was included as a random factor. Appropriate variance structures were selected to account for heteroscedasticity between strata. Normality and homogeneity of residual variances were verified with, respectively, Levene's and Kolmogorov–Smirnov test. WCC decomposition rates were likewise tested for WCC species (WCC), preceding (S14) and current (S15) main crop treatment differences and incubation location (own fallow) following the same protocol.

Dependence among litter traits was tested with Pearson's correlation coefficient. Hereafter, WCC decomposition rate k in fallow plots was regressed against each trait separately to estimate the variance explained by each trait. The relationship between WCC decomposition and litter quality was tested in a full regression model by forward-selecting the traits explaining most additional variance. Block and variance structures were no significant additions to this model. Homogeneity and normality of variances were confirmed.

Changes in abiotic and biotic soil properties in response to rotation treatments (H1b) were tested following the outlined mixed effects protocol (full model: WCC*S14). As abiotic soil properties, we considered SOM, mineral N, potential N mineralisation and pH as response variables. Biotic soil properties included bacterial and fungal biomass, F:B and ergosterol concentration. Treatment effects of rotation on the PLFA profiles were investigated with principle component analysis (PCA, after verifying axis length) and PERMANOVA (10^5 permutations), with backward-selection of the significant factors starting from an additive model (S14+WCC), with strata defined by blocks (vegan package; Oksanen et al., 2016). The influence of abiotic soil properties on the microbial community composition was likewise tested with PERMANOVA (full model: SOM+mineral N+potential N mineralisation+pH).

Decomposition rates of the four standard substrates were tested for effects of preceding main crop, WCC and current main crop (H2a), with mixed effects modelling (full model: S14*WCC*S15). WCC legacy effects on the decomposition rates of the standard substrates and of WCC litters were tested by comparing the decomposition rate of the substrate or litter in a plot with a specific WCC history (h) relative to its decomposition rates in the fallow plot (f) of that same block (b) and same main crop (mc):

$$\text{Relative WCC legacy effect}_{h,b,mc} = \ln \frac{k_{h,b,mc}}{k_{f,b,mc}}$$

Differences between relative WCC legacy effects on litter and standard-substrate decomposition were tested with a mixed linear model including litter type as main factor, with block, preceding- and current main cropping as random factors.

Finally, with multiple linear regression, we tested how decomposition rates of filter paper and rooibos were influenced by the decomposition drivers (H2b): directly through WCC residue turn-over rates (WCC k in fallow) and WCC residue input (shoot biomass), or indirectly through soil abiotic (SOM, mineral N, potential N mineralisation, pH), microbial biomass and composition (bacterial and fungal biomass, F:B, ergosterol and coordinates PCA axis one and two). Filter paper decomposition rates in former *Avena* or *Cichorium* plots were considered separately as was rooibos tea decomposition for current main crop. Filter paper k in former *Avena* plots was ln transformed. Decomposition rate constants were regressed with each explanatory variable separately, with block as random factor. Final regression models for filter paper and rooibos tea decomposition were selected by forward-selecting significant explanatory variables in order of $R^2_{marginal}$ ranking (Johnson, 2014).

3 | RESULTS

3.1 | WCC litter traits

Winter cover crop litters differed significantly in N ($F_{5,62} = 88.01$, $p < 0.0001$), C ($F_{5,62} = 107.60$, $p < 0.0001$) and lignin ($F_{5,62} = 11.69$, $p < 0.0001$) concentration (Figure 1a–c, Supporting Information Table S1). Litter N ranged from 20 mg/g in *Lolium* and *Raphanus* litters to 39 mg/g in the legumes litters. *Raphanus* litter contained least (22 mg/g) and *Vicia* litter contained most lignin (80 mg/g). Carbon content displayed a similar ranking (Figure 1b), with lowest levels for *Raphanus* (404 mg/g) and highest for *Vicia* litters (453 mg/g). Litter traits were significantly positively correlated with each other, including a positive correlation between N and C ($r = 0.35$), and lignin ($r = 0.39$) (Supporting Information Table S2).

3.2 | WCC decomposition rate

Winter cover crop decomposition rates differed significantly between WCC treatments ($F_{5,203} = 109.79$, $p < 0.0001$; Figure 1d, Supporting Information Table S3). In fallow plots *Raphanus* litter decomposed fastest, whereas *Vicia* decomposed slowest. The k values were also influenced by the preceding main crops (S14: $F_{1,203} = 5.62$, $p = 0.0187$) and current main crops (S15: $F_{1,203} = 46.59$, $p < 0.0001$)

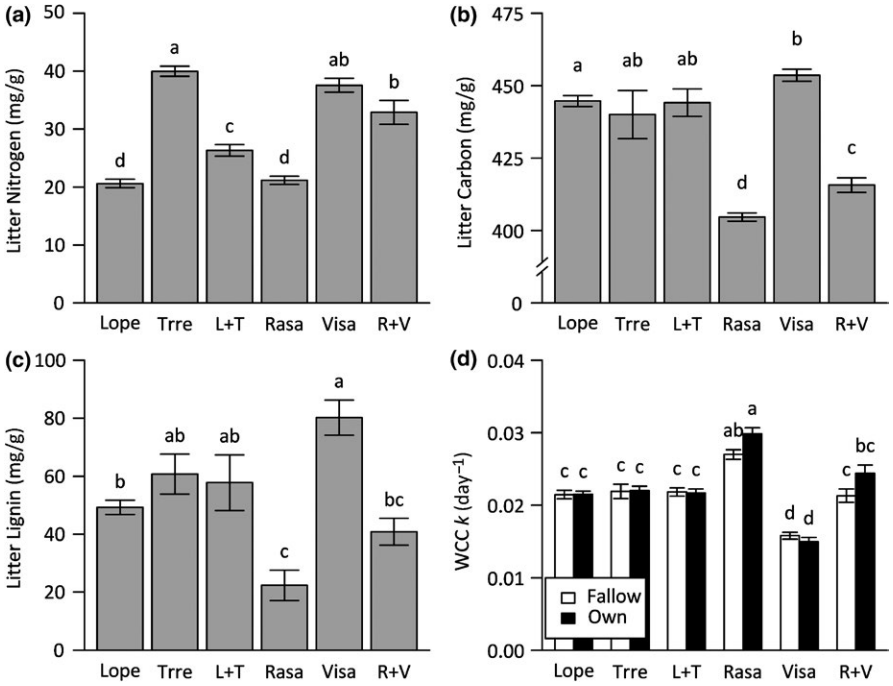

FIGURE 1 Winter cover crop litter traits (a) nitrogen, (b) carbon, (c) lignin concentration and mean decomposition rates (d) in fallow (white bars) or own plots (black bars), ±*SE*. Lope = *Lolium perenne*, Trre = *Trifolium repens*, L + T = *Lolium* + *Trifolium* mixture, Rasa = *Raphanus sativus*, Visa = *Vicia sativa*, R + V = *Raphanus* + *Vicia* mixture. Different letters indicate significant ($\alpha \leq 0.05$) difference based on Tukey post-hoc. $N = 70$ (a–c), in (d) $N = 221$

TABLE 1 Model specification, regressing WCC decomposition rate $k \sim$ Nitrogen + Carbon + Lignin, including sum of squares (SS). Bold values: $p < 0.05$, $R^2_{\text{adjusted}} = 0.4112$, $N = 70$

	SS	Estimate	*SE*	*t*-value	*p*
(Intercept)		0.0518	0.0095	5.454	**<0.0001**
Nitrogen	0.00042	−0.00019	0.000056	−3.483	**0.0009**
Carbon	0.00016	−5.2E-05	0.000023	−2.233	**0.0289**
Lignin	0.00006	−4.2E-05	0.000019	−2.187	**0.0323**

(Supporting Information Table S3). Litters incubated in former *Avena* plots decomposed faster than in plots with a *Cichorium* legacy. Current *Avena* and *Cichorium* cropping had opposite effects: *Avena* presence reduced decomposition compared to *Cichorium* presence. We observed a significant interaction between litter identity and location (own vs. fallow) ($F_{5,203} = 3.18$, $p = 0.0087$). Contrary to our expectations, decomposition of fast-decomposing litters (*Raphanus*, *Raphanus + Vicia*) tended to be elevated in own versus fallow plots (Figure 1d), although not significantly.

To explore how litter quality influenced decomposition rates, WCC *k* in fallow plots was regressed against litter traits (Table 1), therein N concentration explained more variation than C and lignin (N: $R^2 = 0.28$; lignin: $R^2 = 0.25$; C: $R^2 = 0.23$). Overall, WCC decomposition was best explained by a model including all three traits, in which WCC decomposition rate was negatively related to all litter traits.

3.3 | Legacy effects on soil abiotic and biotic properties

Winter cover crop treatments significantly affected the abiotic soil conditions at the start of the *in situ* litter incubation (Supporting Information Table S4). Available mineral N ($F_{6,127} = 4.88$, $p = 0.0002$) and potential N mineralisation ($F_{6,127} = 5.02$, $p = 0.0001$) were highest after *Raphanus* (17.7 mg/kg, resp. 554 μg kg^{-1} day^{-1}), and lowest after fallow and *Lolium* treatments (12.5–12.9 mg/kg, resp. 386.7–412.9 μg kg^{-1} day^{-1}). SOM ($F_{6,127} = 5.07$, $p = 0.0001$) content decreased after *Lolium*. Soil pH did not differ with WCC treatments but displayed small yet significant differences between preceding main crops ($F_{1,127} = 19.84$, $p < 0.0001$), with mean soil pH of 5.75 on former *Avena* and 5.68 on former *Cichorium* plots.

Winter cover crop treatments and preceding main crop identity significantly affected microbial biomass (Table 2), although fungal PLFA marker and ergosterol were low overall. Bacterial and fungal PLFAs were more abundant after *Vicia* than after winter fallow treatments. Preceding *Avena* increased fungal biomass and fungal:bacterial ratios (F:B), compared to preceding *Cichorium* cropping. The WCC on F:B ratios tested significantly, although the post-hoc test did not show significant differences. In line with the PLFA results, ergosterol quantities differed between WCC treatments, although not between preceding crops (Table 2). The ergosterol concentrations were highest after *Raphanus* and lowest after fallow and *Lolium* treatments.

Contrastingly, microbial community composition did not differ between WCC treatments, and was only marginally affected by preceding main crop treatment (PERMANOVA, WCC: $F_{6,129} = 1.33$ $p = 0.117$; S14 $F_{1,129} = 2.64$ $p = 0.0617$, not shown). Variation in microbial community composition related significantly to soil abiotic properties (Supporting Information Figure S2a): SOM explained

TABLE 2 Soil microbial biomass based on PLFA and Ergosterol, and specification of final mixed effects model

	Bacterial PLFA (nmol/g)		Fungal PLFA (nmol/g)		F:B		Ergosterol (mg/kg)	
	M	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
WCC								
Fallow	18.0^{b}	1.2	0.68^{b}	0.05	0.038^{a}	0.001	0.44^{bc}	0.02
Lolium	17.9^{ab}	0.7	0.68^{ab}	0.03	0.038^{a}	0.001	0.43^{c}	0.03
Trifolium	18.6^{ab}	0.8	0.79^{ab}	0.05	0.042^{a}	0.001	0.50^{abc}	0.04
Lolium + Trifolium	18.1^{ab}	0.8	0.69^{ab}	0.05	0.037^{a}	0.002	0.48^{abc}	0.03
Raphanus	19.5^{ab}	0.9	0.75^{ab}	0.04	0.038^{a}	0.001	0.56^{a}	0.03
Vicia	20.6^{a}	0.8	0.84^{a}	0.04	0.040^{a}	0.001	0.51^{abc}	0.02
Raphanus + Vicia	19.0^{ab}	1.0	0.76^{ab}	0.05	0.040^{a}	0.002	0.55^{ab}	0.03
	$F_{6,126}$	2.20	$F_{6,125}$	2.67	$F_{6,125}$	2.23	$F_{6,126}$	3.27
	P	**0.0473**	**P**	**0.0179**	**P**	**0.0443**	**P**	**0.005**
S14								
Avena	19.4	0.5	0.78^{a}	0.02	0.040^{a}	0.001	0.51	0.02
Cichorium	18.3	0.5	0.70^{b}	0.02	0.038^{b}	0.001	0.48	0.02
	—	—	$F_{1,125}$	7.59	$F_{1,125}$	9.338	—	—
	—	—	**P**	**0.0067**	**P**	**0.0027**	—	—
Model specification								
Fixed factors	WCC		WCC+S14		WCC+S14		WCC	
Random structure	Block		Block		Block		Block	
Variance structure	VarIdent on S14		VarIdent on S14		VarIdent on WCC		—	

M ± *SE* given by winter cover crop treatment (WCC) or preceding main crop (S14). Bold values: $p < 0.05$. Different letters indicate significant ($\alpha \leq 0.05$) difference based on Tukey post-hoc, $N = 137$.

8.6% (PERMANOVA $F_{1,133} = 13.03$, $p < 0.0001$) and soil mineral N 4.0% ($F_{1,133} = 6.03$; $p = 0.015$) of the variation; potential N mineralisation and soil pH were not significant factors.

The first PCA axis explained 91.7% of the variation, the second axis only 3.7% (Supporting Information Figure S2). A few PLFA markers were very abundant (Supporting Information Table S5) whereof unspecified marker 16:00 hours and general bacterial marker 16:1ω7c strongly associated with the first axis. PLFA markers for Gram-positive bacteria were found in the lower part of the PCA, of which markers i15:00 and a15:00 had a high abundance. Markers for Gram-negative bacteria associated positively with the second axis, of which 18:1ω7 was found in high abundance.

3.4 | Decomposition of standard substrates

Standard substrates decomposition rates varied widely (Table 3) though not exceeding WCC decomposition rates; average k (day^{-1}) ranked as: filter paper (0.018) > green tea (0.015) > rooibos tea (0.005) > bamboo (0.0008). Decomposition rates of all standard substrates were affected by rotation design, with most pronounced effects for filter paper and rooibos tea. Both substrates decomposed fastest in *Raphanus* and *Raphanus+Vicia* plots and slowest in former fallow plots. Green tea responses were opposite, with lowest rates in *Raphanus*, and *R+V*. Bamboo decomposition rates varied little and responded to the current crop. Furthermore, preceding *Avena* cultivation resulted in significantly decreased decomposition rates of filter paper compared to preceding *Cichorium* cultivation. Although the other substrates were influenced by current main crop presence, with reduced rates in the presence of *Avena* compared to *Cichorium* cropping (Table 3).

3.5 | WCC legacy effects on decomposition

We tested whether WCC legacy effects were specific for substrate quality by comparing decomposition rates of WCC litter and standard substrate incubated in plots with a WCC history to incubation in fallow plots. The relative effect of *Raphanus* and *Raphanus + Vicia* legacies varied significantly between the substrates and own litters (Figure 2b,f). In *Raphanus* plots, filter paper decomposed significantly faster than in fallow plots ($t_{93} = 4.74$, $p < 0.0001$). Also bamboo, rooibos and own *Raphanus* litter tended to decompose faster in former *Raphanus* than fallow plots, although this effect was not significant. Green tea responded barely to WCC legacies. Comparable results were found for *Raphanus + Vicia* plots, in which filter paper decomposed significantly faster than in fallow plots ($t_{94} = 4.08$, $p = 0.0001$). Relative legacy effects for own litters was never larger than those for standard substrates.

To pinpoint the underlying mechanisms, we tested how decomposition drivers (abiotic and biotic soil properties and WCC residue characteristics) influenced decomposition rates of filter paper and

TABLE 3 Standard substrates decomposition rate (*k*). Model specifications *k* of standard substrates across all plots

	Filter paper k (day^{-1})		Bamboo k (day^{-1})		Green tea k (day^{-1})		Rooibos tea k (day^{-1})	
	M	*SE*	*M*	*SE*	*M*	*SE*	*M*	*SE*
WCC								
Fallow	0.0106^{b}	0.0023	0.00079	0.00002	0.0162[1]	0.0004	0.0050^{c}	0.0001
Lolium	0.0147^{ab}	0.0032	0.00077	0.00002	0.0152[1]	0.0004	0.0051^{c}	0.0002
Trifolium	0.0190^{ab}	0.0034	0.00086	0.00003	0.0160[1]	0.0006	0.0055^{c}	0.0002
Lolium + Trifolium	0.0149^{ab}	0.0030	0.00077	0.00002	0.0155[1]	0.0003	0.0053^{c}	0.0001
Raphanus	0.0255^{a}	0.0030	0.00092	0.00005	0.0151[1]	0.0006	0.0063^{a}	0.0002
Vicia	0.0188^{ab}	0.0039	0.00078	0.00002	0.0158[1]	0.0005	0.0054^{bc}	0.0003
Raphanus + Vicia	0.0226^{a}	0.0028	0.00079	0.00002	0.0143[1]	0.0002	0.0062^{a}	0.0002
S14								
Avena	0.0132^{b}	0.0016	0.00083	0.00002	0.0155	0.00026	0.0055[1]	0.0001
Cichorium	0.0188^{a}	0.0017	0.00079	0.00001	0.0154	0.00025	0.0057[1]	0.0001
S15								
Avena	0.0174	0.0017	0.00077^{b}	0.00002	0.0146[1]	0.00023	0.0051[1]	0.0001
Cichorium	0.0188	0.0018	0.00085^{a}	0.00002	0.0163[1]	0.00023	0.0061[1]	0.0001
Model specification								
S14	$F_{1,126}$ **P**	20.59 **<0.0001**	–	–	–	–	$F_{1,125}$ P	1.78 0.1848
WCC	$F_{6,126}$ **P**	3.20 **0.0058**	–	–	$F_{6,121}$ **P**	4.11 **0.0009**	$F_{6,125}$ **P**	9.17 **<0.0001**
S15	–	–	$F_{1,131}$ **P**	35.83 **<0.0001**	$F_{1,121}$ **P**	27.57 **<0.0001**	$F_{1,125}$ **P**	66.69 **<0.0001**
S14*WCC	–	–	–	–	–	–	–	–
S14*S15	–	–	–	–	–	–	$F_{1,125}$ **P**	4.97 **0.0276**
WCC*S15	–	–	–	–	$F_{6,121}$ **P**	2.28 **0.0403**	–	–
S14*WCC*S15	–	–	–	–	–	–	–	–
N	138		137		139		139	

M ± *SE* given by winter cover crop treatment (WCC), preceding (S14) or current main crop (S15). Final linear mixed effect model include specified explanatory variables, with block as random, for green tea a variance structure varIdent (WCC), for Bamboo varComb (WCC + S14). Bold values: $p < 0.05$. Different letters indicate significant ($\alpha \leq 0.05$) difference based on Tukey post-hoc.

[1]For Green tea and Rooibos tea see Fig. S3 for pairwise comparisons of significant interaction terms.

rooibos tea across all plots with a WCC legacy (fallow plots excluded) (Table 4), as filter paper and rooibos tea displayed most pronounced WCC legacy effects. Effects of preceding main cropping treatments on filter paper decomposition and current main cropping on rooibos decomposition were considered separately. Filter paper decomposition incubated in former *Avena* plots was significantly influenced by WCC residue characteristics. Both WCC biomass and litter turn over (i.e. *k* in winter fallow plots) promoted filter paper decomposition. Paper incubated in former *Cichorium* plots was influenced by fungal biomass. Furthermore, rooibos decomposition in current *Avena* plots was stimulated by WCC biomass, whereas decomposition in the presence of *Cichorium* was promoted by the combined effect of WCC biomass and ergosterol concentrations. Neither Filter paper nor rooibos decomposition rates were related to any of the abiotic soil properties.

4 | DISCUSSION

Litter decomposition is influenced by litter quality and soil biotic and abiotic conditions (Austin et al., 2014; Bradford et al., 2016; Cornwell et al., 2008). Answering the question how sequential plant occupation of soil patch influences litter decomposition is essential for carbon and nutrient management. Here, we discuss how WCC legacies influence decomposition drivers, and how decomposition is affected during the growing season following WCC residue incorporation.

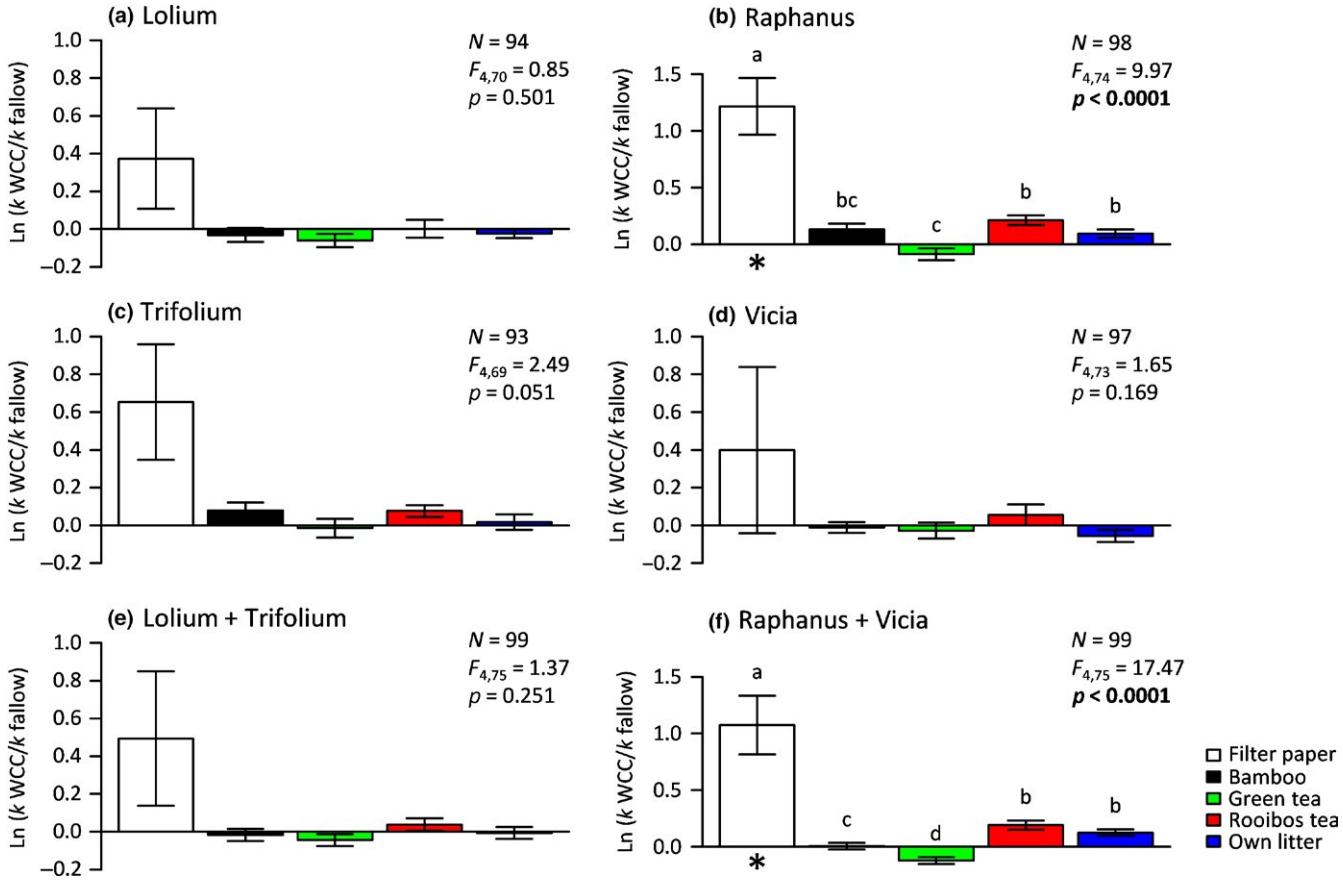

FIGURE 2 Winter cover crop (WCC) legacy effect on decomposition rates of standard substrates and own litter incubated in indicated WCC plot compared to incubation in winter fallow plots. Positive values indicate higher decomposition rate (*k*) in WCC field than in fallow, and vice versa. Note: *y*-axis scaled differently for readability. Mean relative effects ± *SE*. Different letters indicate significant difference between litters based on Tukey post-hoc test. *Significant difference from zero

4.1 | WCC litter quality and decomposition

Litters with low C:N ratios usually decompose fast, as do litters with low lignin concentrations (Freschet et al., 2012b; Palm, Giller, Mafongoya, & Swift, 2001). We found that WCC decomposition rates related negatively with lignin, C and surprisingly also N concentrations. According to plant-economic spectrum theory (Cornwell et al., 2008), fast-growing plants are expected to have high N concentrations and low levels of structural compounds, such as lignin. However, our legume litters showed high lignin as well as high N concentrations. Legumes have higher lignin concentrations compared to grasses (Cherney, Johnson, Volenec, & Anliker, 1988), grain and mustard cover crops (Ramirez-Garcia, Gabriel, Alonso-Ayuso, & Quemada, 2015). The high legumes representation in our species pool contributed to the negative correlation between litter N concentration and decomposition rates.

We collected WCC litters as above-ground biomass in December, whereas in practice WCC residues include roots and are incorporated into the soil in February. Inevitably, the residue quality that actually entered the soil will vary from the presented litter quality, but is expected to differ in a coordinated fashion across the WCC treatments (Freschet, Cornelissen, van Logtestijn, & Aerts, 2010). Therefore, our litter quality should be interpreted as an approximation.

4.2 | Legacy effects on local abiotic and biotic conditions

The history of main crops and especially WCCs created varying start conditions for the litter decomposition experiment. Changes in soil mineral N and potential N mineralisation result from N uptake and mineralisation during the WCC growing season and shortly after incorporation. Especially *Raphanus* productivity contributed to an elevated soil N pool (Barel, Kuyper, de Boer, et al., 2018), which may be attributed to high level of N scavenging, productivity and rooting depth (Thorup-Kristensen et al., 2003). Preceding main crop-induced little differences in abiotic conditions except in soil pH, which was slightly higher in preceding *Avena* compared to *Cichorium* plots. We consider this slight difference as inconsequential.

Plant legacies can also alter microbial biomass and community composition. Overall, our fungal biomass was lower compared to Hedlund (2002), whereas bacterial biomass in our soils was somewhat higher. Low fungal biomass could result from regular soil disturbance typical for agriculture (Stahl, Parkin, & Christensen, 1999). Nevertheless, our microbial biomass (bacterial and fungal PLFA markers) and ergosterol concentrations supported our expectation

TABLE 4 Final multiple linear mixed regression models for decomposition rates (*k*) of filter paper and rooibos tea as function of decomposition drivers

Paper	Slope	*SE*	*df*	*F*	*p*	$R^2_{marginal}$
Avena '14*						
WCC biomass	0.0022	0.001	1,49	8.34	**0.0057**	0.210
WCC k_{fallow}	75.433	28.005	1,49	7.26	**0.0097**	
Cichorium '14						
Fungal Bm	−0.136	0.063	1,46	12.19	**0.0011**	0.326
Ergosterol	0.031	0.013	1,46	8.01	**0.0069**	
F:B	3.397	1.165	1,46	3.92	0.0538	
PC1	−0.053	0.023	1,46	5.49	0.235	
Rooibos	**Slope**	*SE*	*df*	*F*	*p*	$R^2_{marginal}$
Avena '15						
WCC biomass	2.06×10^{-6}	0.67×10^{-6}	1,53	9.577	**0.0031**	0.142
Cichorium '15						
WCC biomass	2.58×10^{-6}	0.92×10^{-6}	1,50	11.8211	**0.0012**	0.229
Ergosterol	0.00181	0.000815	1,50	4.9325	**0.0309**	

**k* for paper incubated in former *Avena* plots were ln transformed.
Bold values: p < 0.05.

to rank with WCC biomass input. Microbial biomass values were highest for *Raphanus*, *Vicia* and *R+V*, consistent with their aboveground biomass (Barel, Kuyper, de Boer, et al., 2018). Partial senescence of *Vicia* plants early in winter could have stimulated the microbial community differentially from other WCCs. Moreover, *Avena* residues likely have a higher C:N ratio than *Cichorium*, which could stimulate saprotrophic-fungal biomass. Indeed, fungal PLFA concentrations and F:B ratio were higher in preceding *Avena* than in preceding *Cichorium* plots.

In addition, we tested for rotation legacy effects on the microbial community composition by PLFA analysis. Community differences were mostly driven by PLFA 16:0, strongly associated with PCA axis 1. This straight-chained PLFA, also known as palmitic acid, is a frequently occurring lipid of divers origin (Ruess & Chamberlain, 2010). Contrasting to our hypothesis, rotation history did not significantly influence microbial community composition. Instead, SOM and soil mineral N were significant predictors, indicating that changes in abiotic and biotic soil conditions go hand-in-hand. WCC treatments and to a lesser extend previous main crop treatments affected soil microbial biomass directly, and could indirectly influence microbial community composition through legacy effects on abiotic soil properties. Although PLFA analysis is a well-established method for the quantification of broad functional microbial groups, it is less sensitive to changes in community composition compared to techniques for measuring taxonomic diversity (e.g. high-throughput sequencing). Therefore, small shifts in community composition could have been missed, which could signify long-term changes (Brennan & Acosta-Martinez, 2017; Chavarría et al., 2016).

4.3 | WCC legacy effects on decomposition

Home-field advantage literature proposes that home-incubated litters decompose faster due to adaptation of the local soil community. Recalcitrant litters should benefit most from home incubation, as decomposition of these litters require a more specialised decomposer community (Wallenstein et al., 2013). Conversely, our results suggest a stimulation of decomposition in plots with easily decomposable WCCs, as rates of fast-decomposing WCC litters tended to be enhanced when decomposing in their home-plot. This stimulation appeared to be non-specific as WCC legacies also influenced decomposition rates of newly added standard substrates of different qualities. Relative to fallow, *Raphanus* and *Raphanus+Vicia* legacies stimulated decomposition of standard substrates filter paper and rooibos tea, even more so than of the home litters. In other words, the magnitude of legacy effects depends on the identity of the WCC leaving the legacy as well as the substrate quality. The stimulation of filter paper decomposition rather than home litter decomposition suggests that WCC legacy effects on decomposition did not rely on specific adaptation of the local soil community to home litters and are the result of increased overall abundance and/or activity of the saprotrophic microbial community.

In natural ecosystems, HFA varies in both strength and direction (Veen et al., 2015). For specialisation of the decomposer community to occur a clear "litter quality" signal is required (Ayres et al., 2009; Freschet et al., 2012a; Veen et al., 2015). In agricultural systems, temporal diversification through crop rotation likely increases the diversity of litters thereby promoting general activity of decomposers rather than selecting for specialised saprotrophic microbes (McDaniel, Grandy, Tiemann, & Weintraub, 2014, 2016).

The underlying mechanisms of WCC-induced stimulation of decomposition were explored by regressing WCC litter characteristics, soil biotic and abiotic conditions to filter paper and rooibos tea decomposition. WCC residue biomass and inherent turn-over rate as well as microbial biomass and community composition could be main mechanisms through which (cover) crop legacies acts upon decomposition of organic substrates. Crop residue quality and microbial

community could explain the observed preceding main crop effects on WCC and filter paper decomposition. Decomposition of cellulose in filter paper is primarily limited by N availability. Remaining low-quality crop residues (e.g. preceding *Avena*) possibly immobilised N (Parton et al., 2007), thus restricting paper decomposition. Alternatively, WCC litters had much lower C:N ratios than cellulose and instead benefited from the higher microbial biomass in former *Avena* plots. Experimental manipulation of microbial biomass and nitrogen availability are recommended to provide a causal test of our findings.

Furthermore, the current main crops influenced decomposition of WCC litters, bamboo, green- and rooibos tea. Present plants can decrease decomposition by offering preferred resources (Saar, Semchenko, Barel, & de Deyn, 2016), or by competing for nitrogen (Bek, 1994). In addition, effects of main crop presence on decomposition can be due to microclimatic differences (see Supporting Information). Despite irrigation, current *Avena* plots had lower soil moisture content than *Cichorium* plots during the second half of the experiment, probably reducing decomposition (Prescott, 2010). The main crop influence on decomposition illustrates that success of soil fertility management with WCCs depends on the context of the whole rotation. How the dynamics of WCC litter decomposition and mineralisation synchronise with the nutrient demands of subsequent crops, and how WCC litter decomposition contributes to the build-up of SOM over time are topics for further study.

5 | CONCLUSIONS

Carbon and nutrient cycling in agroecosystems differ from natural systems because of increased disturbances and high nutrient supply. Here, we show that the choice of WCC in crop rotation influences decomposition of both own and newly added organic residues. This effect is generated directly via the quantity and quality of WCC residues, as productive WCCs with labile litters can potentially form positive litter feedback loops through the general stimulation of the microbial community. In addition, WCC that increase fungal biomass promote decomposition. Indirectly, WCC can mediated changes in SOM and soil mineral N which, in turn, influence the soil microbial community composition. Inclusion of WCC in rotation designs, offers scope for management of carbon and nutrient cycling in agricultural systems, through WCC litter feedbacks. Furthermore, assessment of temporal nutrient-cycling dynamics during the growing season can benefit from information on crop residue quantity and quality as well as general decomposer activity.

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AUTHORS' CONTRIBUTIONS

J.M.B., T.W.K., W.B. and G.B.D.D. conceived the ideas and designed the experiment. J.M.B., G.B.D.D. and J.P. executed the experiment and data collection. J.M.B. analysed the data. J.M.B. and G.B.D.D. led the writing, to which all authors contributed. The final manuscript was approved by all authors.

DATA ACCESSIBILITY

Data available via the Dryad Digital repository https://doi.org/10.5061/dryad.pk5n1p4 (Barel, Kuyper, Paul, et al., 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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