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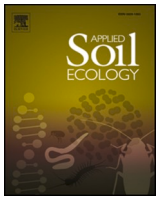

Impact of soil inoculation on crop residue breakdown and carbon and nitrogen cycling in organically and conventionally managed agricultural soils

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ABSTRACT

Organic agriculture relies on organic fertilizers and amendments to provide nutrients to plants and will therefore depend on decomposer communities to release nutrients from these organic inputs. However, after conversion of conventional to organic agriculture it may take up to decades before decomposer communities become adapted to the new resource inputs. The aim of the present study is to investigate if the functional capacity of soil communities for decomposing recalcitrant crop residue types can be enhanced by inoculating soil communities from organically into conventionally managed soils. We used a microcosm incubation experiment to test how soil inoculation, agricultural management history, and crop residue type affect carbon and nitrogen cycling with crop residue addition. We collected soil samples from 5 pairs of conventional and nearby organic fields and set up a reciprocal inoculation experiment under controlled lab conditions. We inoculated soil from each conventional field with soil from the paired organic field and vice versa. To each soil mix, five types of crop residues were added: a cover crop mixture, carrot leaves (*Daucus carota*), alfalfa (*Medicago sativa*), hay (*Lolium perenne*), and straw (*Triticum aestivum*). There was one control treatment without any addition. Soils were incubated for 34 days and we measured mass loss of the crop residues from litter bags, cumulative soil respiration, cumulative potential plant available nutrients, permanganate oxidizable carbon (POXC), and substrate-induced respiration (SIR). Initial soil abiotic conditions (soil organic matter content, pH, C:N ratio, plant available nutrients), soil microbial biomass and soil bacterial and fungal community composition were also determined. We did not find clear effects of inoculation on mass loss and cumulative respiration. Instead, effects of crop residue type on all parameters were substantial. Crop residues with higher C:N ratios generally had lower mass loss and cumulative respiration, and resulted in lower nitrogen availability but higher POXC contents. Organic management enhanced cumulative respiration. There was little overlap in bacterial and fungal ASVs between the organic and conventional soils within each pair, resulting in a potential increase in diversity as a result of soil inoculation. We conclude that decomposition of crop residues declined with their recalcitrance, and that soils from organically managed fields did not increase the capacity of the soil community to decompose recalcitrant residues. Further studies are needed to determine whether compositional differences between soils from organic and conventional fields are a response to farming practices or whether management also has functional implications for soil fertility.

Abbreviations: SIR, substrate-induced respiration; POXC, permanganate oxidizable carbon.

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1. Introduction

The use of mineral fertilizers in agriculture has resulted in higher yields (Dunwell, 2013; McArthur and McCord, 2017) at the expense of soil biodiversity (Tscharntke et al., 2012; Tsiafouli et al., 2015; Wall et al., 2015), and has enhanced nutrient losses to the ground and surface water and to the atmosphere (de Vries et al., 2013; Rehman and Farooq, 2023). Therefore, there is interest to reduce the amount of mineral fertilizer and instead enhance nutrient provisioning from organic inputs, e.g., organic fertilizers and (cover) crop residues (Bommarco et al., 2013; Tittonell, 2014). Such organic fertilizers need to be decomposed and mineralized by the soil food web to make nutrients available for plant uptake (Bonanomi et al., 2020). Efficient mineralization relies on a well-functioning soil food web (Hannula and Morriën, 2022). However, earlier work has shown that it may take a decade or more for soil communities and functions to respond to land use change (Gerrits et al., 2023; Morriën et al., 2017). Likewise, it has been proposed that it takes time for the soil community to change during conversion from conventional to organic agriculture (Schrama et al., 2018). The challenge is determining how to reduce this conversion time.

Soil microbes are essential for carbon and nitrogen cycling (Creamer et al., 2022; Jiao et al., 2019; Nielsen et al., 2011). The functional capacity of the microbial community can be a key factor driving the rate of decomposition of crop residues that are varying in carbon-to-nitrogen (C:N) ratios (Cornwell et al., 2008; Huang et al., 2023; Osburn et al., 2022; Šantrůčková et al., 2006). Decomposer communities might become specialized toward complex organic inputs (Bonanomi et al., 2020; Fanin et al., 2016; Keiser et al., 2014; Veen et al., 2021). Many fungi are capable of producing extracellular enzymes to degrade recalcitrant carbon compounds, so that more recalcitrant organic inputs also select for more fungal-based soil food webs (Haubert et al., 2009; Op De Beeck et al., 2021; Sharma et al., 2024; Sünnemann et al., 2021). This changed role of soil fungi is supported by findings of higher fungal biomass in organically managed soils (Birkhofer et al., 2008; Esperschutz et al., 2007; Morugán-Coronado et al., 2022; Santos et al., 2012). Therefore, it is expected that soils from organic farms contain decomposer communities that are better able to degrade organic inputs than those from conventional farms.

As the composition and functioning of decomposer communities in conventionally managed soils may not suffice to decompose recalcitrant organic matter (Bonanomi et al., 2016; Postma et al., 2008; Yang et al., 2021), the question is whether the capacity of these communities can be altered by introducing microbes from organically managed soils (Creamer et al., 2015; Janvier et al., 2007; Mallon et al., 2015; Sun et al., 2016; Tedersoo et al., 2014). Translocation of individual microbial taxa to enhance plant nutrient uptake, such as arbuscular mycorrhizal fungi or plant growth-promoting bacteria, has received considerable attention, but success rates are variable and often context-dependent (Mawarda et al., 2020; Ouahmane et al., 2007; Román et al., 2018; Tamayo-Vélez and Osorio, 2018; Trabelsi and Mhamdi, 2013). Inoculations may work under controlled experimental conditions (Hoeksema et al., 2010), but in a fully developed soil community in the field it may be hard for single species to become established (Mallon et al., 2015; Robinson et al., 2024; van Elsas et al., 2012). Recent work in natural ecosystems has shown that inoculations with whole soils from reference fields may effectively change the capacity of target soils to perform functions (Gerrits et al., 2023; Middleton and Bever, 2012; Wubs et al., 2016). However, the potential of soil inoculation for steering decomposer communities, thereby influencing their carbon and nitrogen cycling functions in agricultural soils, has been explored relatively little.

The aim of the present study was to test how soil inoculation affects soil carbon and nutrient cycling in agricultural soils. We set up a full-factorial, 34-day soil inoculation experiment in the laboratory, where we inoculated conventionally managed soils with 10 % soil from nearby fields under organic management, and vice versa. Our main hypothesis was that inoculation of organic soil into conventionally managed soils enhances decomposition of crop residues and therefore increase mass loss and cumulative respiration, particularly of crop residues with higher C:N ratios (Cleveland et al., 2014). In contrast, we expected no effect on decomposition of crop residues with high C:N ratios when inoculating conventionally managed soils into organic soils, because microbial communities from conventional soils were not expected to have higher functional capacity for decomposition. Further, we expected that the enhanced decomposition of organic inoculations would be accompanied by enhanced nitrogen availability for plants and microbes, as well as enhanced microbial biomass, as measured by SIR.

2. Materials and methods

2.1. Soil sampling

Soils were collected in October 2018 from sandy fields in the east of the Netherlands near Oploo and Deventer (Table A.1). The year of conversion is the year in which the organic farmers converted from conventional to organic farming (Table A.1). Soils were classified as Anthrosols with a very low elutriable fraction and an A-horizon of at least 30 cm. We collected soil samples from 5 organic and 5 conventional fields, which were collected in pairs. The fields from each pair were located as close as possible to each other, so that soil conditions were as comparable as possible. In each field, soil cores (0–30 cm) were taken from 3 subplots with a minimum distance of 25 m between the cores, and the subplots were 10 m away from the field edge. The soil cores from the three subplots in each field were combined to a composite sample per field. Soil was transported in a cooler box, stored at 4 °C, and sieved the day after collection using a 4 mm mesh.

2.2. Experimental set-up

We filled 500 mL air-tight pots, fitted with gas-sampling septa, with 230 g dry-weight equivalent soil. There were four soil mixtures prepared using the paired soils: 100 % organic, 100 % conventional, 90 % organic plus 10 % conventional, and 90 % conventional plus 10 % organic. 5–15 % of soil inoculum is common practice, and strikes a balance between transferring sufficient micro-organisms to influence the receiving community whilst having only negligible effect on soil fertility (Adikane et al., 2006; De Long et al., 2023; Kapagianni et al., 2019; van der Putten et al., 1988). Handling the soils and mixing was done using sterilized tools.

Five crop residues were selected to provide a range in C:N ratio. Moreover, these residues originate from crops that are commonly grown in agricultural fields in North-Western Europe which are generally left on the field (Arcand et al., 2016; Hu et al., 1997; Marschner et al., 2011). The five crop residues were a cover crop mixture, carrot leaves (*Daucus carota*), alfalfa (*Medicago sativa*), hay (*Lolium perenne*), straw (*Triticum aestivum*). We purchased the crop residues commercially, except for the cover crop mixture, which was grown at a sandy field near Wageningen. This was the TERRALIFE® - SOLARIGOL-mixture from DSV Zaden (DSV Zaden, Venzelderheide). Before the addition of the crop residues to the pots, all residues were dried at 70 °C and cut into 5–10 mm pieces. For all residues, 25 % was put into a litter bag and the remainder was mixed gently through the soil. In addition, for each inoculation treatment there were control pots without crop residues. The controls were created and treated as all other experimental units. In total, there were 120 pots: 5 replicates × 2 management types (organic vs. conventional) x 2 inoculation treatments (with vs. without) x 5 crop residue types plus 1 no-residue control. The amount of residue added to each pot was standardized based on C content, with an addition of 1.04 gC / 230 g soil.

Litter bags were buried in the soils and pots were placed for 34 days in the dark in a climate-controlled chamber at 18 °C at 65 % of water holding capacity. We left the lids of the pot slightly open to prevent moisture loss, but allow gas diffusion. Pot positions were randomized.

2.2.1. Crop residue characteristics

To determine the C content of the crop residues, we collected three subsamples for each residue, which were ground using a TissueLyser II (Qiagen, Hilden Germany and measured for total C and N content using a CN elemental analyser (Interscience flashEA© 1112 series). In total each pot received 2.78 g carrot leaves (*Daucus carota*), 2.73 g cover crop mixture, 2.58 alfalfa (*Medicago sativa*), 2.67 g hay (*Lolium perenne*) and 2.47 g wheat straw (*Triticum aestivum*). As the amount of added residue was standardized by carbon, the amount of added nitrogen varied between the crop residues and ranged from 0.013 g N for wheat straw to 0.116 g N per pot for the cover mixture (Table A.2).

2.3. Initial soil analyses

Fresh soil was used for pH-water determination. We used 40 °C dried soil (five days) for analyses of plant available phosphate, soil organic matter and carbon-to-nitrogen-ratio. Freeze-dried soil was used for phospholipid fatty acids (PLFA) extraction.

2.3.1. pH

We mixed 10 g dry weight equivalent fresh soil with 25 mL of demineralized water by shaking soil and water for 2 h at 250 rpm, followed by determining pH using a laboratory pH meter (Mettler Toledo).

2.3.2. P-Olsen

Plant available phosphate (PO_4-P content (mg/kg dry soil)) was determined by a 0.5 M NaHCO3 extraction at pH 8.5, 1:20 *w/v*), also known as the P-Olsen (Olsen et al., 1954). Plant available orthophosphate was measured using the SEAL QuAAtro Segmented Flow Analysis (SFA) Auto Analyser (Murphy and Riley, 1962) (Beun de Ronde, Abcoude).

2.3.3. Soil organic matter

Soil organic matter (SOM) content was determined by mass loss on ignition. Samples were dried for 24 h at 105 °C and then placed in a muffle furnace for 8 h at 430 °C. SOM content was calculated as the weight difference between samples heated at 105 °C and 430 °C.

2.3.4. Carbon-to-nitrogen element ratios

To determine the C:N ratio of the soil, dried soil was first ground to a fine dust using the TissueLyser II (Qiagen, Hilden Germany). 5–6 mg of ground soil was weighed and put into a small tinfoil cup. Carbon and nitrogen were analysed by elemental analyser (Interscience flashEA© 1112 series).

2.3.5. Plant available nitrogen

To determine the plant available mineral nitrogen, 10 g dry weight equivalent fresh soil plus 50 mL of 1 M KCl were shaken for 2 h at 250 rpm (Mettler Toledo) (Keeney and Nelson, 1983). We measured concentrations of NH_4^+, NO_3^- and NO_2^- in the solution with a SEAL QuAAtro Segmented Flow Analysis (SFA) Auto Analyser (Beun de Ronde, Abcoude).

2.3.6. PLFA

Phospholipid fatty acids (PLFA) were extracted from 2.5 g of freeze-dried soil into a single-phase chloroform/methanol/citrate buffer, pH 4.0 (Bligh and Dyer, 1959; Frostegård et al., 1991). The extract was split into two phases by the addition of water. The organic phase was purified by solvent extraction, then dried and redissolved in chloroform. PLFAs were separated by solid phase extraction on a silica column (Strata SI-1, Phenomenex) by elution with methanol after less polar lipids were eluted with chloroform and acetone. A 19:0 methyl ester internal standard was added before converting the eluted phospholipids into fatty acid methyl esters using alkaline methanol (0.2 M KOH). After derivatization the methyl esters were extracted into hexane and a second internal standard (12:0 methyl ester) was added. Methyl esters were separated on a GC Trace 1300 coupled to a TSQ 8000 mass spectrometer (Agilent VF-5MS column, 20 m length, 0.15 mm ID, 0.30 µm film thickness; 1 µL (injection; helium carrier gas; full scan 50–300 *m/z*). Identification and quantification were performed by comparison to set of external standards run alongside the experimental samples. Fatty acid markers selected as indicative for bacteria were: i15:0, ai15:0, i16:0, 16:1w7c, i17:0, cy17:0, cy19:0 (Joergensen, 2022; Norris et al., 2023; Willers et al., 2015). The marker for fungi was 18:2w6c (Frostegård and Bååth, 1996). Results are expressed in µg fatty acid / g dry soil.

2.4. Communities of bacteria and fungi

2.4.1. DNA isolation

DNA was extracted from frozen soil (−80 °C) using Powersoil DNA extraction kits (Qiagen) following the manufacturer's instructions. Amplicon library preparation and sequencing was performed by Génome Québec. The prokaryotic 16S gene V4 region was amplified with the forward and reverse primers 515F (Parada et al., 2016) and 806R (Apprill et al., 2015), and fungal ITS2 region with forward primer ITS4ngs and compound reverse primers ITS3tagmix (Tedersoo et al., 2015). These amplicon libraries were sequenced in separate flow cells on an Illumina MiSeq PE250 instrument.

2.4.2. Sequence processing

Raw reads were demultiplexed and adaptor sequences removed by the sequencing company. The 16S amplicon sequences were processed using the DADA2 pipeline, version 1.20 (Callahan et al., 2016), during which primers were removed by trimming, and forward and reverse reads were truncated to 230 and 200 bases, respectively, quality filtered (parameters maxN = 0, maxEE = c(2,2), truncQ = 2, rm.phix = TRUE) and chimeric sequences removed. Taxonomy was assigned using the SILVA SSU database (version 138.1) (Quast et al., 2012).

ITS sequences were analysed using the PIPITS pipeline (version 2.8, standard settings) (Gweon et al., 2015). This pipeline merged read pairs (PEAR) and quality filtered, then extracted the ITS2 region with ITSx (Bengtsson-Palme et al., 2013), with short reads (<100 bp) removed. Fungal OTUs were clustered (97 % sequence identity) and chimeric sequences were removed by comparing with UNITE UCHIME database (version 8.2) (Edgar et al., 2011). Sequences were classified using with RDP against the UNITE fungal database (Kõljalg et al., 2013; Nilsson et al., 2019).

2.4.3. Sequence data preparation

Low abundant Amplicon Sequence Variants (ASVs) with one read were removed as potential sequencing artefacts (Auer et al., 2017). Sequences identified as non-bacterial and non-fungal were removed from the dataset as well. Then, we rarefied the data to 1978 reads for 16S and to 2657 reads for ITS.

2.5. Functions

2.5.1. Mass loss

Mass loss was calculated by the percentage mass loss of the contents of the litter bags. Litter was weighed when placed in the litter bags. After the incubation, litter was removed from the litter bags, washed and put in paper bags to dry. After 48 h of drying at 70 °C the weight was determined again. Percentage mass loss was expressed as a percentage of added weight.

2.5.2. Cumulative respiration

Respiration was measured as CO_2 accumulation in the head space of the microcosms. This was done on days 1, 3, 4, 7, 10, 14, 23 and 32. Before collecting the samples, we closed the lids for four hours. Then we took a 12 mL headspace gas sample using a syringe and 0.6 mm needle. Samples were kept in pre-evacuated 6 mL exetainers. CO_2 concentration was measured using a Trace GC ultra (Thermo Scientific, Waltham US).

Standards with known CO_2 concentrations were made to create a calibration line.

2.5.3. Cumulative potential available nitrogen

Cumulative potential plant available mineral nitrogen was measured using resin bags buried in the pots (Binkley and Matson, 1983). Resin bags were constructed of nylon stockings, and contained 10 g of a 1:1 mixture of cation and anion exchange resins, preloaded with H^+ and Cl^-, respectively. We determined the plant available mineral nitrogen (NO_3^-, NO_2^- and NH_4^+), retained by the resin during incubation. Any adhering soil was brushed off the resin bags and they were extracted with 50 mL of 1 M KCl with shaking for 2 h at 250 rpm (Mettler Toledo). We measured concentrations of NH_4^+, NO_3^- and NO_2^- in the solution with a SEAL QuAAtro Segmented Flow Analysis (SFA) Auto Analyser.

2.5.4. SIR

Substrate induced respiration (SIR) was measured as a proxy for microbial biomass (Anderson and Domsch, 1978; Bååth and Anderson, 2003). Approximately 4.8 g of fresh soil of each sample was weighed in airtight sealed containers with a rubber penetrable lid. An extract of autolyzed yeast cells (*Saccharomyces cerevisiae*) (Thermo Scientific, United States) was added to each container. The containers were flushed with CO_2 free air and incubated for 4 h. Thereafter, a headspace gas sample was transferred into exetainers with a syringe and the amount of CO_2 in each exetainer was analysed with a TRACE 1310 gas chromatograph. The CO_2 produced by the biota per g dry soil per hour was calculated as $\mu g\ CO_2\ g^{-1}\ h^{-1}$.

2.5.5. POXC

For analysis of POXC (Culman et al., 2012; Weil et al., 2003), 20 mL of 0.02 mol L^{-1} $KMnO_4$ were added to 50 mL polypropylene screw-top centrifuge tubes containing 2.5 *g* of 2 mm sieved air-dried soil. The tubes were shaken for exactly 2 min at 240 oscillations/min and allowed to settle for exactly 10 min, after which 0.5 mL of the supernatant was transferred into a second 50 mL centrifuge tube and mixed with 49.5 mL of deionized water. Sample absorbance was read with a spectrophotometer at 550 nm and POXC (mg/kg soil) was calculated based on absorbance:

$$POXC\ (mg\,kg^{-1}) = \frac{(0.020\ mol\,L^{-1} - (a + (b \times Abs_{adj})) \times (9000\ mg\,mol^{-1}) \times (0.02\ L)}{Soil\ mass\ (kg)}$$

where 0.02 mol L^{-1} is the initial concentration of the $KMnO_4$ solution, *a* is the intercept of the standard curve (which was 0), *b* is the slope of the standard curve, which was 0.0473 for the batch of initial soil samples and 0.0462 for the batch of samples after the experiment. *Abs* is the absorbance of the unknown soil sample, 9000 mg is the amount of C oxidized by 1 mol of MnO_4^- with Mn^{7+} reduced to Mn^{4+}, 0.02 L is the volume of $KMnO_4$ solution reacted with soil.

2.6. Statistics

2.6.1. Initial soil (a)biotic conditions and crop residue characteristics

Paired *t*-tests were used to test how organic versus conventional management affected initial biotic and abiotic soil characteristics. Differences in bacterial and fungal community composition between conventional and organic management were tested by permutational ANOVA (perMANOVA) based on Bray-Curtis distances. These were visualised using non-metric multidimensional scaling (NMDS). Differences in carbon (C), nitrogen (N) and C:N ratio between substrates were tested using ANOVA.

2.6.2. Effects of crop residues, management and soil inoculation on mass loss and C and N related processes and properties

There was considerable variation between fields. Therefore, we present the effects of crop residue addition on soil carbon and nutrient variables as the log response ratio (log RR) = ln(crop residue/control), where control is without addition of crop residues. We calculated this separately for each type of crop residue within each field (Hoeksema et al., 2010; Jayne and Quigley, 2014). Values of log RR above 0 indicate that crop residue addition increased the variable under consideration relative to the control without residue addition. In contrast, a negative log RR indicates that the addition of residues resulted in values lower than the control. For mass loss we could not calculate response ratios to control for variation between fields within pairs, because no measurement can be collected from soil without addition of amendments.

A one-sample t-test was performed on the log response ratios to test whether they differed from zero, which would indicate that crop residue addition significantly impacted the variable under consideration relative to the control treatment without crop residue addition. Effects of crop residue types, management and soil inoculation on carbon and nutrient related properties and processes were tested using a three-way ANOVA followed by Tukey's HSD test. These were performed on both raw data and on the log response rations.

Data analysis was performed in R version 4.3.2 (R Core Team, 2023). For post hoc tests we used the functions lsmeans and cld from the "multcomp" package (Bretz et al., 2002).

3. Results

3.1. Initial soil (a)biotic conditions and crop residue characteristics

Substrate-induced respiration (SIR) was lower in organically than in conventionally managed soils (t-test: $t = 2.86$, df = 6, 88, $p = 0.025$). Organically and conventionally managed soils did not significantly differ in any other abiotic properties, bacterial and fungal richness, diversity or PLFA contents (t-test: $p > 0.05$, Table A.1, Table A.3).

Initial bacterial and fungal community composition generally were not different between organic and conventional management (Fig. A.1). However, within a pair, only 0–11 taxa out of the 344–627 bacterial ASVs were overlapping between organically and conventionally managed soils, while 98–336 ASVs were not overlapping, the overlap was thus below 5 % (Table A.4). For fungal OTUs, within a pair, only 82–99 taxa out of the 399–417 fungal ASVs were overlapping between organically and conventionally managed soils, whereas 96–235 ASVs were not overlapping, which indicates <25 % of the ASVs were overlapping (Table A.4). Therefore, while there were no general management effects, all fields still had quite unique bacterial and fungal ASV composition. Since maximally 25 % of the taxa was shared between soils within a pair, soil inoculation had the potential to increase species richness of both bacteria and fungi (Table A.4).

The C:N ratio differed between crop residue types (Table A.2; $F_{4,10} = 197{,}082$, $p < 0.001$), which was mostly caused by differences in N content ($F_{4,10} = 289$, $p < 0.001$); all crop residues had quite similar carbon content (Table A.2; $F_{4,10} = 2.86$, $p = 0.081$). The cover crop mixture had the lowest C:N ratio, followed by carrot leaves, alfalfa and hay, while straw had the highest C:N ratio (Table A.2).

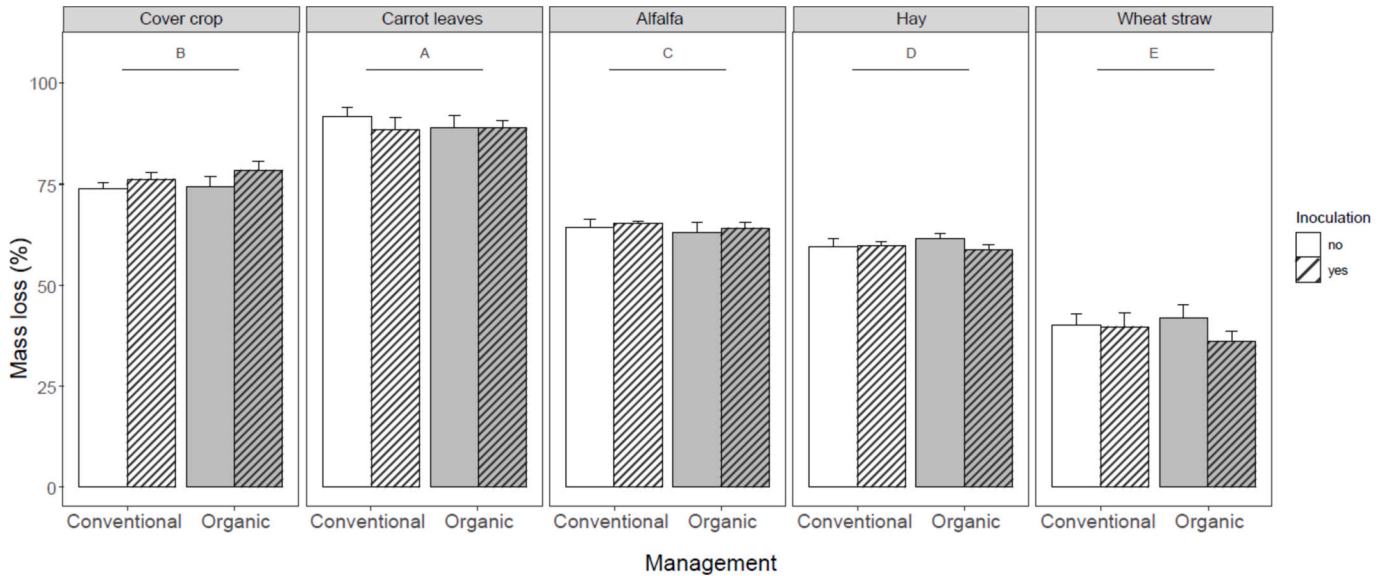

Fig. 1. Mass loss of crop residues. Mass loss of crop residues is affected by the type of crop residues, and not by land management (conventional versus organic) or inoculation with the reciprocal soil (no or yes). All crop residue types were significantly different from each other indicated by the capital character in the upper left corner, this was tested by a Tukey post hoc test. Y-axis represents the fraction of mass that was lost during incubation. White bars are soils with conventional management history, grey bars are soils with organic management history. Hatched bars are inoculated soils, so 10 % soil from the contrasting management type. Substrates are ranked from left to right in order of low to high C:N ratio. Therefore, carrot leaves had the highest mass loss, but only the one-but lowest C:N ratio.

3.2. Effects of soil inoculation, crop residues and management on mass loss and C and N related processes and properties

Mass loss of the crop residues was affected mainly by the type of residue, with mass loss generally decreasing with increasing C:N ratios ($F_{4,80} = 274.12$, $p < 0.001$). Carrot leaves had the highest mass loss, followed by the cover crop mixture, alfalfa and hay and straw had the lowest mass loss. There was no effect of soil inoculation on mass loss of crop residues ($F_{1,80} = 0.10$, $p = 0.748$) and neither effects of management ($F_{1,80} = 0.09$, $p = 0.763$). Also, no interaction effects between soil inoculation, management, and crop residue type on mass loss of crop residues were observed (Fig. 1).

The impact of residue additions (log RR) on cumulative respiration were higher in soils with an organic than a conventional management history (Fig. 2; $F_{1,80} = 21.46$, $p < 0.001$). However, inoculation of organic into conventional soil did not increase cumulative respiration to the same level as in whole organic soil (Fig. 2; Table 1). All log RR of cumulative respiration were higher than zero indicating that addition of crop residues to soils enhanced respiration (Fig. 2; $F_{4,80} = 9.28$, $p < 0.001$). For straw addition, which had the highest C:N ratio (Table A.2), log RRs for cumulative respiration were lower than for the other four crop residue types (Fig. 2). Absolute cumulative respiration data confirmed the patterns observed in the log RRs, with straw having lower absolute respiration values than the other crop residues (Table A.5, Table A.6; ANOVA: $F_{5,96} = 421.04$, $p < 0.001$). However, in contrast to the log RRs, we did not find effects of organic versus conventional soil management on absolute values (Table A.5, Table A.6).

Generally, compared to the control, straw and alfalfa decreased cumulative nitrogen availability, whereas carrot leaves, cover crop and hay incubation had more cumulative nitrogen availability (Table 1, Fig. 2). The impact of residue addition (log RR) on cumulative available mineral nitrogen was affected by a 3-way interaction between crop residue type, management and soil inoculation (Table 1, Fig. 2). Absolute cumulative nitrogen availability was also affected by a three-way interaction of crop residue type, management and inoculation (Table A.5, Table A.6). Cumulative nitrogen availability was twice as much with the cover crop mixture as with carrot leaves. Alfalfa and hay were not different from the control. Straw incubation, through which the lowest amounts of nitrogen are added, resulted in a 5–9-fold lower cumulative nitrogen availability than in the control treatment. In case of the cover crop mixture, carrot leaves and alfalfa, organic soil inoculum enhanced cumulative nitrogen availability. However, there was no effect of organic versus conventional soil management when adding hay or straw. For cover crop, soil inoculation decreased absolute cumulative nitrogen availability in soils with a conventional management history.

The impact of residue addition (log RR) on substrate-induced respiration (SIR) differed between organic and conventional, as well as between crop residue types. However, there was no effect of soil inoculation (Table 1, Fig. 2). In general, log RRs were highest for non-inoculated incubations of cover crop and carrot leaves, intermediate for hay and alfalfa and lowest for the wheat straw incubation with soil inoculation. Log RRs of cover crop and carrot leaves were greater than zero, indicating that addition of these lowest C:N ratio residues enhanced SIR. In contrast, wheat straw addition, which has the highest C:N ratio, resulted in negative log RRs, indicating that it decreased SIR (*t*-test: $t = -5.265$, $df = 19$, $p < 0.001$). Log RR for SIR were lower in organic than in conventional soils ($F_{1,80} = 8.69$, $p = 0.004$). Interaction effects were not significant. The absolute values of SIR were highest for soils with cover crops and carrots, intermediate for soils with alfalfa or without residues and lowest for soils incubated with hay and wheat straw. However, SIR in soils with hay was not significantly different from the control. Also, absolute numbers of SIR were lower in organic than in conventional, but not different between soils with and without inoculation (Table A.5).

The log RRs for POXC were affected by residue type and soil inoculation, but not by agricultural management (Table 1, Fig. 2). Soil inoculation had a positive effect on log RRs regardless of substrate type and management. This shows that substrate addition enhanced POXC in inoculated soils compared to uninoculated soils. However, this was independent of conventional versus organic soil management, because inoculation resulted in higher POXC amounts after substrate addition in both organic and conventional soils. In general, POXC log RRs were greater than zero for hay and straw, indicating that for these substrates the POXC content was increased in soils compared to control soils without the substrate. For the other substrates, the log RRs did not differ from zero, indicating that the POXC content was not significantly

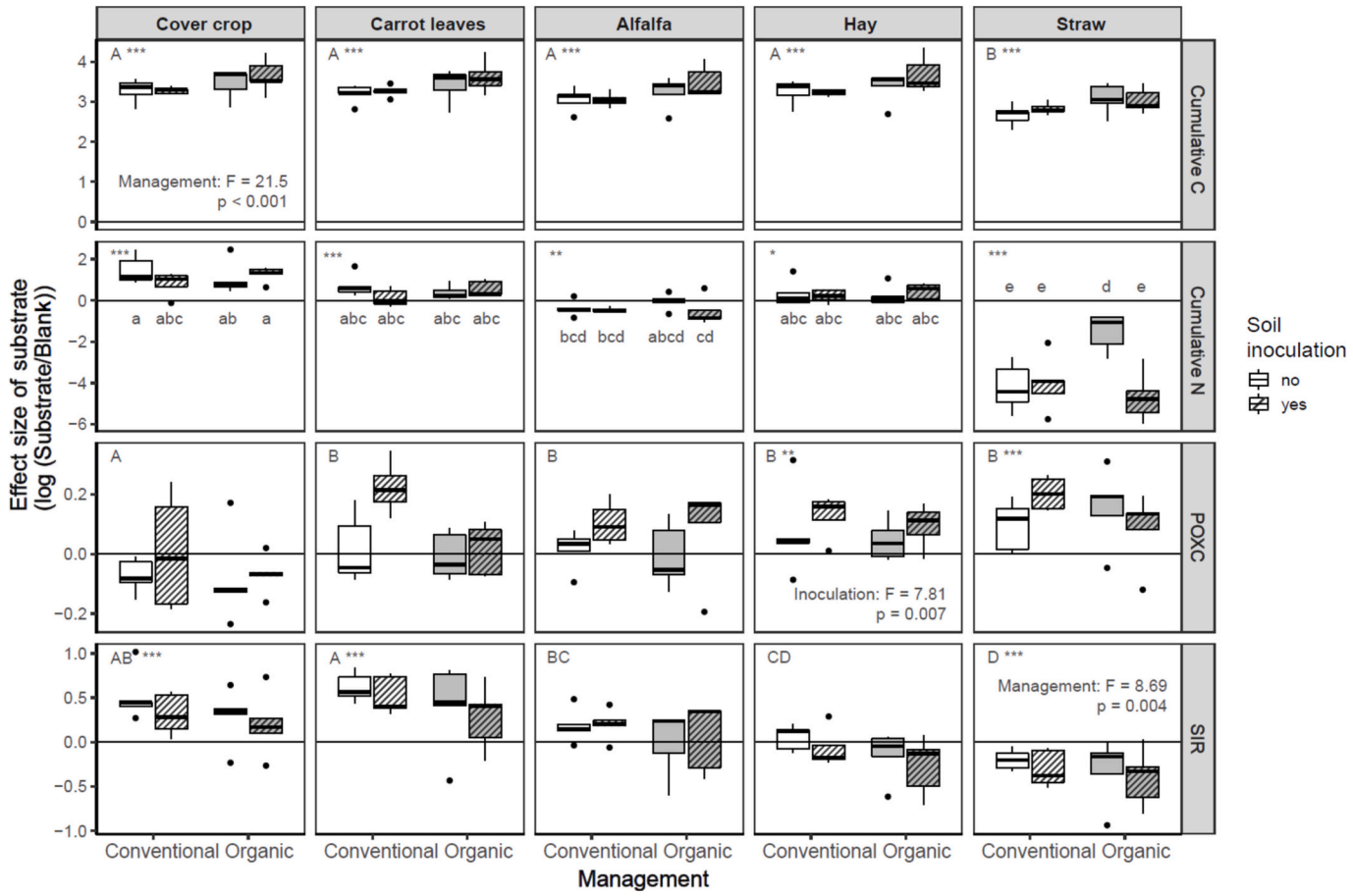

Fig. 2. Log-response ratios of crop residues. Log response ratios of crop residue types of cumulative carbon and nitrogen mineralization during incubation, permangate oxidizable carbon (POXC) and substrate induced respiration (SIR) right after incubation. White bars are soils with conventional management history, grey bars are soils with organic management history. Hatched bars are inoculated soils, so 10 % soil from the contrasting management type. Substrates are ranked from left to right in order of low to high C:N ratio. Therefore, carrot leaves had the highest mass loss, but only the one-but lowest C:N ratio. The control treatment has been set as zero, which is indicated by a horizontal line in each panel. Boxes above the zero line indicate that the values of the substrates where higher than the control, boxes below the zero line indicate that the values of the substrates where lower than the control. Capital characters in each left corner indicate the differences between crop residue types (each presented in a separate panel), and significant differences between crop residue types and the control are indicated by stars behind the capital characters. */**/*** indicate the level of significance (*≥ 0.05, **≥ 0.005, *** = 0.0005). Small characters above the boxes indicate differences between boxes, comparing all interactions, so they were only applied if interactions were at place.

Table 1
Effects of crop residue type, management and soil inoculation on log response ratios of crop residue types of cumulative carbon and nitrogen mineralization, permangate oxidizable carbon (POXC) and substrate induced respiration (SIR). Log RRs are calculated as ln(result crop residue / result control).

log RR substrates		Cumulative C		Cumulative N		POXC		SIR	
	df	*F*	*p-value*	*F*	*p-value*	*F*	*p-value*	*F*	*p-value*
Type of crop residue	4	9.28	**<0.001**	150.46	**<0.001**	7.86	**<0.001**	22.52	**<0.001**
Management	1	21.46	**<0.001**	3.50	0.065	3.49	0.066	8.69	**0.004**
Soil inoculation	1	3.22	0.076	10.01	**0.002**	7.81	**0.007**	2.17	0.145
Type of crop residue: Management	4	0.01	1.000	2.01	0.102	0.49	0.741	0.12	0.975
Type of crop residue: Soil inoculation	4	0.07	0.991	3.96	**0.006**	0.60	0.662	0.32	0.863
Management: Soil inoculation	1	1.30	0.258	1.71	0.195	3.71	0.058	0.08	0.779
Type of crop residue:Management: Soil inoculation	4	0.57	0.685	8.18	**<0.001**	0.80	0.526	0.04	0.996
Residual degrees of freedom	80								

affected by substrate addition. There were no significant interactions between crop residue type, conventional versus organic soil management and inoculation on the log RRs of POXC content after substrate addition (Table 1, Fig. 2). In the absolute POXC data, there were no significant effects of substrate addition, soil inoculation, soil management or their interactions on POXC content, probably because variation was relatively high (Table A.1, Table A.5).

4. Discussion

Efficient cycling of soil carbon and nitrogen is key for sustainable agriculture where less external inputs are needed for generating yield. The use and type of crop residues and the microbial communities responsible for their decomposition are essential for efficient carbon and nutrient cycling (Cleveland et al., 2014; Luo et al., 2018). However,

relatively little is known about how decomposer communities and crop residues interactively affect carbon and nitrogen cycling in soils from organically managed fields, which are usually assumed to be more capable of decomposing recalcitrant organic matter than soils from conventionally managed fields. The aim of our study was therefore to test how soil inoculation in combination with the addition of crop residues affects carbon and nitrogen cycling in soils from fields under organic versus conventional management. We expected that inoculation of organic soil, including the decomposer soil community, into conventional soil would enhance carbon and nitrogen cycling, particularly for crop residues of lower quality (i.e., high C:N). This is because organic soils are generally associated with higher decomposition rates (Bonanomi et al., 2016; Hu et al., 1997), and microbial communities in organically managed soils might have specialized on the degradation of more recalcitrant inputs from organic fertilizers (Bonanomi et al., 2016; Gomiero et al., 2011). In our study, soil inoculation had however limited impacts, while there were major effects of crop residue type on soil carbon and nutrient cycling. The more recalcitrant crop residue types (i.e., high C:N ratios) generally had low mass loss, cumulative respiration and resulted in a lower nitrogen availability and higher POXC content, while the more labile ones had high mass loss, cumulative respiration and nitrogen availability.

Organic management did not impact mass loss nor nitrogen availability in our experiment, which is in contrast to expectations (Fanin et al., 2016; Rashid et al., 2013). However, management had an impact on respiration. Organic management resulted in higher rates of cumulative respiration but in lower rates of substrate-induced respiration than conventional management. The lack of significant differences between organic and conventional management could be due to the high variation among arable fields. This variation might be caused by historical differences in management that are more field specific than general for either conventional or organic management (Naveed et al., 2016; Quist et al., 2019; van Rijssel et al., 2022).

In contrast to our expectation that soil inoculation could stimulate soil functioning (Robinson et al., 2024; Román et al., 2018; Wubs et al., 2016) and would particularly favour the breakdown of crop residues with higher C:N ratios (Cleveland et al., 2014; Op De Beeck et al., 2021; Sharma et al., 2024), we found that inoculation effects were generally absent. This finding aligns with our results that management effects on mass loss and most of the carbon and nutrient cycling variables were also absent. Hence, a lack of initial differences in soil abiotic and biotic properties and in functioning between conventional and organic, might be an explanation for the absence of an inoculation effect.

Alternatively, inoculation might have been ineffective because the added microbes did not establish well after inoculation, as establishment of organisms in field soils where there is already a soil community present can be challenging (Mallon et al., 2015; van Elsas et al., 2012). Successful examples of soil inoculation in nature restoration projects have often been applied to sites where top soils were removed (Gerrits et al., 2023; Wubs et al., 2019; Wubs et al., 2016), which creates opportunities for the newly added soil communities to develop. Generally soil biodiversity restoration may take one to several decades (Gerrits et al., 2023; Morriën et al., 2017). Moreover, although communities might change fast, it can take a while before the impact on functions such as mass loss can be detected (Veen et al., 2021). Our experiment might simply have been too short to identify effects of inoculation on soil carbon and nutrient cycling. Finally, it could also be that the introduction of larger organisms such as earthworms and arthropods, of which some subgroups are more abundant in organic agriculture, could have stronger effects on decomposition (Chassain et al., 2024; Crittenden et al., 2014; Irmler, 2010; Lubbers et al., 2017).

Despite the lack of initial differences between conventional and organic management of the field soil, we still found an effect of inoculation in two cases. First, there was a three-way interaction effect for cumulative potential available mineral nitrogen. Second, there was a direct positive effect of inoculation on POXC content. POXC content was enhanced by soil inoculation after substrate addition, both in soils with conventional and with an organic management history. A question that arises is whether POXC and cumulative potential available mineral nitrogen will be more sensitive parameters than the rate of decomposition itself. POXC is only a small fraction of the carbon pool in soil, but was proposed as an indicator of partly decomposed labile carbon (Hurisso et al., 2016; Thoumazeau et al., 2020) and being correlated to bacterial diversity (Ramírez et al., 2020). Our work supports the view that POXC is a sensitive measure that responds to arable management (Bongiorno et al., 2019; Fine et al., 2017; Morrow et al., 2016). However, it is still unclear what this really means for C and nutrient cycling, as it is highly debated how to interpret changes in POXC (Margenot et al., 2024; Woodings and Margenot, 2023).

The type of crop residues affected all measured indicators of carbon and nitrogen cycling. As expected, residues with low C:N ratios, and thus high quality to decomposers, had high mass loss and cumulative respiration, while those with high C:N ratios, had low mass loss and cumulative respiration (Cleveland et al., 2014; Cookson et al., 1998; Flavel and Murphy, 2006; Heijboer et al., 2016; Šantrůčková et al., 2006). Crop residues with high C:N ratios, like wheat straw, reduced SIR and cumulative nitrogen availability, whereas they enhanced POXC content over the duration of this study. Initial reduced nitrogen availability after the incubation of crop residues with high C:N ratios is also known as nitrogen immobilization. Immobilized nitrogen is not sensitive to leaching and might become available for plant uptake at later moments. Thus, initial reduced nitrogen availability due to wheat straw residues might actually be more sustainable, depending on the timing of crop demands (Delin and Engström, 2010; Pang and Letey, 2000; van der Sloot et al., 2022).

5. Conclusions

We conclude that most crop residues enhanced carbon and nitrogen availability for plants and microbes, potentially supporting plant nutrition and soil health. However, while some effects of organic versus management were observed, soil inoculation of soils from organic fields to soils from conventional fields generally had limited effects on carbon and nitrogen cycling. This is contrary to our expectation that soil communities from organic fields would be better capable of mineralizing rest products from crops, particularly those with high C:N ratios, than soil communities from conventional fields. Our findings might be explained by limited initial differences between conventional and organic soils, the short duration of the study, or poor establishment of newly added microbial communities in live field soil. Longer-term studies are needed to unravel the potential of soil inoculation for steering soil communities for decomposition of recalcitrant crop residues in agricultural fields.

CRediT authorship contribution statement

Sophie Q. van Rijssel: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Eva Kuipers:** Data curation, Conceptualization. **Kyle Mason-Jones:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Guusje J. Koorneef:** Writing – review & editing, Conceptualization. **Wim H. van der Putten:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **G.F. (Ciska) Veen:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: W.H. van der Putten reports financial support was provided by Dutch Research Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

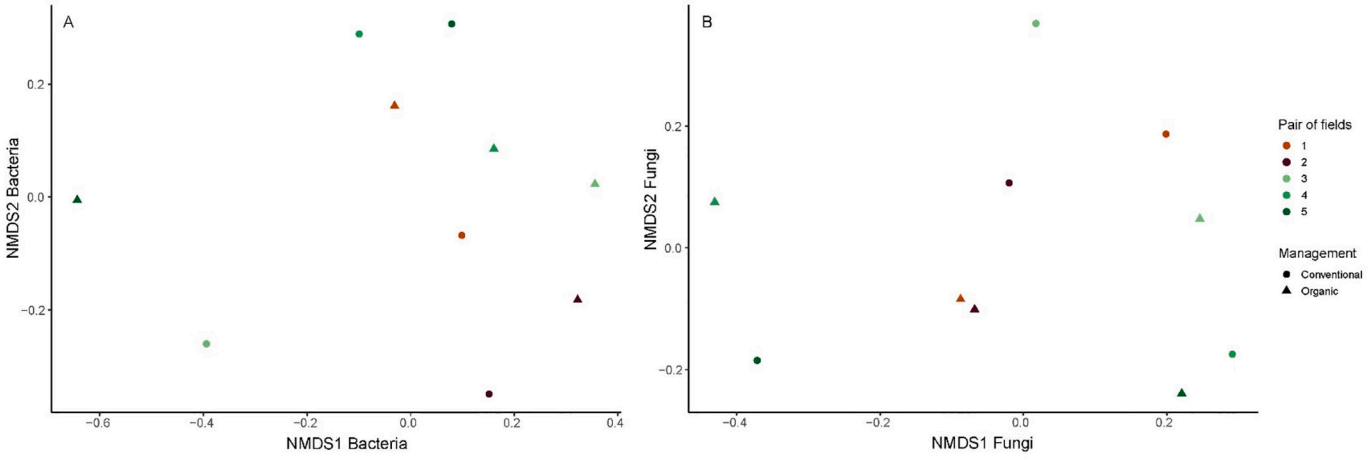

Fig. A.1. NMDS plot of bacterial (A) and fungal (B) community composition on based on Bray–Curtis dissimilarity. Management and replicate of paired fields were not affecting bacterial composition (perMANOVA: management: $F_{1,9} = 0.96$, $p = 0.868$; pair: $F_{4,9} = 1.00$, $p = 0.33$) and fungal composition (perMANOVA: management: $F_{1,9} = 0.79$, $p = 0.712$; pair: $F_{4,9} = 0.83$, $p = 0.835$). Dimensions and stress values are the following: Bacteria: k = 2, stress = 0.12; Fungi: k = 2; stress = 0.11. Circles represent conventionally managed fields, while triangles represent organically managed fields, colors indicate the pair.

Table A.1
Edaphic information on sampled fields. There are ten fields in total; Five pairs, indicated by "replicate", of an organically and a conventionally managed arable field.

	Replicate	Management	Year of conversion	Coordinates	pH	P-Olsen	SOM	POXC	CN-ratio	NO3	NH4
						mg/kg	%	mg/kg		mg/kg	µg/g
SO021	1	Organic	1930	51°34′N 5°48′E	6.4	102	3.34	335	17.3	36.2	0.42
SC021	1	Conventional	1930	51°33′N 5°49′E	5.3	124	4.18	302	13.6	96.0	0.64
SO061	3	Organic	1976	52°16′N 6°19′E	6.2	73	3.09	364	13.6	6.4	0.22
SC061	3	Conventional	1976	52°14′N 6°14′E	6.6	83	3.79	429	13.8	12.1	0.36
SO521	4	Organic	1994	52°25′N 6°13′E	5.6	117	4.38	245	14.8	12.8	0.46
SC521	4	Conventional	1994	52°22′N 6°15′E	6.3	69	3.42	104	13.6	7.4	0.55
SO052	5	Organic	1999	52°14'N 6°14′E	6.7	79	3.37	83	12.8	6.8	0.42
SC052	5	Conventional	1999	52°14′ N 6°14′E	5.6	88	3.72	225	11.6	24.5	0.52
SO051	2	Organic	2013	52°14'N 6°14′E	6.4	46	4.01	379	13.7	6.3	0.43
SC051	2	Conventional	2013	52°14'N 6°14′E	5.6	101	3.45	200	13.1	6.2	0.37

Table A.2
Mean values (± standard deviation) for chemical properties of each crop residue type. Significant differences between crop residues were tested by ANOVA and are indicated by *** ($p < 0.0001$). Follow-up Tukey's HSD results are shown as letters in superscript (if applicable).

Common name	Latin name	Carbon (%)	Nitrogen (%)***	C:N ratio***	Added N (g)
Cover crop mixture	[−]	38 ± 0.06	3.68 ± 0.01^{a}	10.3 ± 0.06 ^{a}	0.102 ± 0.0030
Carrot leaves	*Daucus carota*	37.4 ± 0.04	3.15 ± 0.00^{b}	11.9 ± 0.00^{b}	0.087 ± 0.0006
Alfalfa	*Medicago sativa*	40.2 ± 0.06	2.55 ± 0.01^{c}	15.8 ± 0.06^{c}	0.067 ± 0.0006
Hay	*Lolium perenne*	41.7 ± 4.83	2.25 ± 0.27^{c}	18.5 ± 0.11^{d}	0.06 ± 0.0007
Wheat straw	*Triticum aestivum*	42.1 ± 0.11	0.54 ± 0.00^{d}	78.2 ± 0.21^{e}	0.013 ± 0.0001

Table A.3
Biotic information on sampled fields.

	Replicate	Management	Year	SIR	Bacterial richness	Shannon diversity bacteria	Fungal richness	Shannon index fungi	PLFA Bacteria	PLFA Fungi
				µg/g/h					µg/g	µg/g
SO021	1	Organic	1930	70	343	5.5	254	4.1	2.0	0.08
SC021	1	Conventional	1930	119	291	5.4	242	3.7	3.3	0.11
SO061	3	Organic	1976	52	277	5.2	239	3.6	2.4	0.11
SC061	3	Conventional	1976	97	281	5.3	256	3.7	2.1	0.14
SO521	4	Organic	1994	83	98	4.1	256	3.8	1.9	0.06
SC521	4	Conventional	1994	70	246	5.1	256	4.6	2.1	0.08
SO052	5	Organic	1999	56	231	5.0	272	4.3	2.6	0.14
SC052	5	Conventional	1999	80	122	4.3	226	3.8	2.1	0.07
SO051	2	Organic	2013	62	254	5.1	321	4.6	2.7	0.12
SC051	2	Conventional	2013	102	224	5.1	182	3.4	2.2	0.06

Table A.4
Overview of shared and management-specific bacterial and fungal ASVs.

			Bacteria			Fungi		
Replicate	Total ASVs in pair:	Specific in conventional	Specific in organic	Shared	Total ASVs in pair:	Specific in conventional	Specific in organic	Shared
1	627	284	336	7	399	145	157	97
2	472	218	248	6	417	96	235	86
5	352	121	230	1	402	130	176	96
3	547	270	266	11	413	174	157	82
4	344	246	98	0	413	157	157	99

Table A.5
Carbon and nutrient cycling related properties and processes in all treatments; means ± standard deviation. "Inoculation" = inoculation of 10 % of soil from the contrasting managed field from the same pair. Associated statistics can be found in Table A.6. Differences between crop residue types, management and inoculation were tested using a three-way ANOVA (Table A.6) followed by Tukey's HSD test. Within each soil property or process, numbers within columns followed by different letters are significantly different at $p < 0.05$.

Substrate	Management	Soil inoculation	Cumulative respiration	NO3 + NH4 concentration in resin bag	SIR	POXC
			g/pot	mg/L	µg/g/h	mg/kg
Control	Conventional	No	0.09 ± 0.05^{a}	53.5 ± 35.3^{defgh}	61.6 ± 21.2^{abcde}	351 ± 70^{a}
Control	Conventional	Yes	0.08 ± 0.02^{a}	55.7 ± 18.3^{defgh}	52.6 ± 9.4^{abcde}	340 ± 108^{a}
Control	Organic	No	0.10 ± 0.03^{a}	30.9 ± 14.4^{efgh}	57.3 ± 7.2^{bcde}	338 ± 48^{a}
Control	Organic	Yes	0.10 ± 0.01^{a}	44.7 ± 11.8^{efgh}	57.9 ± 26.7^{bcde}	328 ± 32^{a}
Cover crop	Conventional	No	2.76 ± 0.28^{bc}	182 ± 57.5^{a}	88.5 ± 30.6^{f}	297 ± 90^{a}
Cover crop	Conventional	Yes	2.82 ± 0.21^{b}	104 ± 29.5^{bcd}	71.1 ± 10.8^{agh}	320 ± 80^{a}
Cover crop	Organic	No	2.76 ± 0.21^{bc}	124 ± 18.5^{bc}	73.6 ± 6.5^{gh}	320 ± 35^{a}
Cover crop	Organic	Yes	2.66 ± 0.24^{bcd}	132 ± 19.4^{ab}	81.1 ± 11.0^{fh}	308 ± 53^{a}
Carrot leaves	Conventional	No	2.65 ± 0.31^{bcd}	67.4 ± 32.6^{def}	95.2 ± 24.0^{abc}	319 ± 87^{a}
Carrot leaves	Conventional	Yes	2.67 ± 0.36^{bcd}	72.3 ± 28.0^{cde}	92.7 ± 14.5^{abg}	375 ± 72^{a}
Carrot leaves	Organic	No	2.58 ± 0.33^{bcd}	60.9 ± 17.4^{defg}	87.9 ± 19.6^{abcd}	337 ± 36^{a}
Carrot leaves	Organic	Yes	2.66 ± 0.18^{bcd}	70.1 ± 15.7^{cde}	79.2 ± 7.0^{abg}	364 ± 29^{a}
Alfalfa	Conventional	No	2.25 ± 0.20^{cd}	42.6 ± 37.0^{efgh}	64.5 ± 10.6^{bcde}	340 ± 101^{a}
Alfalfa	Conventional	Yes	2.19 ± 0.21^{de}	34.7 ± 20.7^{efgh}	71.3 ± 12.5^{bcde}	342 ± 74^{a}
Alfalfa	Organic	No	2.18 ± 0.10^{de}	24.7 ± 17.4^{efgh}	55.9 ± 10.3^{bcde}	348 ± 22^{a}
Alfalfa	Organic	Yes	2.31 ± 0.18^{cd}	33.4 ± 14.3^{efgh}	60.2 ± 5.3^{bcde}	360 ± 47^{a}
Hay	Conventional	No	2.66 ± 0.10^{bcd}	56.0 ± 25.8^{defgh}	51.5 ± 6.1^{abcde}	350 ± 80^{a}
Hay	Conventional	Yes	2.64 ± 0.18^{bcd}	62.0 ± 22.9^{defg}	53.8 ± 5.4^{abcd}	340 ± 90^{a}
Hay	Organic	No	2.51 ± 0.23^{bcd}	57.7 ± 7.8^{defgh}	46.2 ± 2.8^{abcde}	370 ± 40^{a}
Hay	Organic	Yes	2.75 ± 0.04^{bc}	57.4 ± 10.0^{defgh}	48.7 ± 5.5^{abcde}	388 ± 74^{a}
Straw	Conventional	No	1.61 ± 0.45^{f}	12.3 ± 21.8^{fgh}	42.4 ± 7.7^{cde}	377 ± 94^{a}
Straw	Conventional	Yes	1.69 ± 0.30^{ef}	6.98 ± 14.3^{gh}	45.4 ± 7.1^{de}	368 ± 74^{a}
Straw	Organic	No	1.64 ± 0.21^{f}	4.10 ± 7.64^{h}	37.4 ± 1.4^{e}	374 ± 30^{a}
Straw	Organic	Yes	1.67 ± 0.17^{ef}	1.84 ± 3.24^{h}	39.6 ± 2.2^{e}	385 ± 30^{a}

Table A.6
Effects of crop residue type, management and inoculation on carbon and nutrient cycling related properties and processes.

	Mass loss			Cumulative C			Cumulative N			POXC			SIR	
	df	F	p-value	df	F	p-value	F	p-value	F	p-value	F	p-value	F	p-value
Crop residue type	4	274.12	<0.001	5.00	421.04	<0.001	67.10	<0.001	2.10	0.072	34.83	<0.001		
Management	1	0.09	0.763	1.00	0.20	0.657	4.29	0.041	0.51	0.479	4.95	0.029		
Soil inoculation	1	0.10	0.748	1.00	0.97	0.327	0.61	0.436	0.44	0.509	0.08	0.780		
Crop residue type:Management	4	0.27	0.899	5.00	0.16	0.976	0.33	0.895	0.24	0.943	0.49	0.782		
Crop residue type:Soil inoculation	4	1.22	0.309	5.00	0.21	0.957	2.27	0.054	0.34	0.890	0.64	0.673		
Management:Soil inoculation	1	0.11	0.745	1.00	0.40	0.528	4.91	0.029	0.00	0.973	0.73	0.395		
Crop residue type:Management: Soil inoculation	4	0.60	0.661	5.00	0.57	0.720	2.51	0.035	0.19	0.967	0.90	0.488		
Residuals	80			96.00										

Data availability

Metadata is available after submission in the Dryad Digital Repository: https://doi.org/10.5061/dryad.70rxwdc72. Sequencing data will been submitted to the European Nucleotide Archive (accession number: PRJEB82719). Code availability: the source code of R for model fitting is in the supplement and will be available on GitHub at: https://github.com/SophievanRijssel/APSOIL-D-24-01514R1.

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