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RESEARCH ARTICLE

Rhizosphere-induced shift in the composition of bacterial community favors mineralization of crop residue nitrogen

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Abstract

Aims In agricultural systems, residue amendment is an important practice for nutrient management, but the role of microbes in mineralization of crop residue nitrogen (N) is not well known. Therefore, this study aimed to examine how the residue N mineralization was associated with changes of the microbial community composition in crop rhizosphere.

Methods A rhizobox system was deployed to separate the rhizosphere zone into the root-growth (central), and 2 mm (proximal) and 4 mm (transitional) zones away from the central zone, and the gradient change of the residue-N mineralization along the zones was assessed. Soybean plants were grown in a Mollisol without or with amendment of ^{15}N-labelled soybean and maize residues. Furthermore, amplicon sequencing was performed to detect the shift of microbial community composition associated with the residue-N mineralization.

Results The residue-N was mineralized faster in the rhizosphere than the bulk soil, and from soybean residue than maize residue. Greater enrichment of taxa against the unit of residue-N mineralization in the soybean than maize residue treatment was correspondent with the enriched ammonification genes, likely contributing to the enhanced mineralization of soybean residue-N in the rhizosphere. A gradual increase in dissolved organic C and a decrease in available N concentration from the central root zone to the bulk soil, might shift bacterial community favoring the residue-N mineralization in the rhizosphere.

Conclusions The spatial changes in chemical properties across the rhizosphere lead to the recruitment of microbiome taxa to enhance the mineralization of N derived from crop residues.

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Introduction

In agricultural systems, residue amendment is an important part of cropland management to sustain soil fertility (Pittelkow et al. 2015; Zheng et al. 2022), because crop residues contain large amounts of nutrients, particularly nitrogen (N); for example, maize residues contained 40 − 80 kg N ha^{-1} equivalent (Burgess et al. 2002). Thus, the mineralization of residue-N likely changes soil N cycling (Burgess et al. 2002). The concentration of N in crop residues also influences residue decomposition and subsequent N turnover in soils (Abiven et al. 2011; Li et al. 2020). Nitrogen concentrations in maize and soybean residues differ markedly, ranging from 6.6 to 14 and from 22 to 41 mg N g^{-1}, respectively (Abera et al. 2019; Ding et al. 2019; Hall et al. 2019; Hu et al. 2015; Li et al. 2017, 2018). Soybean residues with higher N concentrations and lower C/N ratios are expected to decompose faster than maize residues. For example, Hall et al. (2019) found that soybean residue decomposed 10–38% faster than maize residue in a loam soil during 193 days of incubation.

The crop rhizosphere, an interface between living roots and soil and the hotspot of biochemical processes, may considerably alter the mineralization of residue-N via a rhizosphere priming effect (RPE) (Wang et al. 2003). The RPE is defined as a change in soil organic matter decomposition rate in the vicinity of living roots compared to the bulk soil (Huo et al. 2017) as a result of changes in microbial activity and function induced by root exudates and/or rhizodeposits (Vargas et al. 2020; Yu et al. 2017). The RPE either accelerates or suppresses the residue decomposition. For example, the residue decomposition is enhanced in the rhizosphere of plant species such as white lupin, rye and maize through stimulation of microbial activity and enzyme productions by rhizodeposits (Cheng and Kuzyakov 2005; Xu et al. 2019). In contrast, the process of residue decomposition is suppressed in the rhizosphere of species such as *Avena barbata* and *Lolium perenne* as plant roots secrete labile organic substances that microorganisms prefer to metabolize over residues (Bird et al. 2011; Castanha et al. 2018; Cheng and Kuzyakov 2005).

Possible effects of the rhizosphere on the mineralization of residue-N may depend on the preference and capability of microbial communities on the residue decomposition (Bird et al. 2011; Castanha et al. 2018; Cheng and Kuzyakov 2005). In the rhizosphere, the plant-C efflux and low N availability due to plant uptake may shift the microbial community composition to mine N from residues, given that low N availability tends to facilitate the decomposition of high-quality residues in terrestrial ecosystems (Knorr et al. 2005; Murphy et al. 2015; Huo et al. 2017). By phospholipid fatty acid (PLFA) analyses, Bird et al. (2011) demonstrated that the turnover of dead roots was stimulated near the living roots of *Avena barbata* compared with the bulk soil, and gram-positive bacteria were likely involved in the residue-N mineralization in the rhizosphere. The change in microbial community composition in the rhizosphere may alter the pace of residue-N mineralization, which has been seldomly addressed up to now compared to the effects of crop residue amendment on microbial community in the bulk soils (Lian et al. 2016, 2019; Li et al. 2020). Moreover, there is a lack of the comparative work on the rhizodeposit-induced change in microbial capability to mineralize N from various crop residues differing in their chemical properties (such as C/N ratio). Thus, studying spatial variations in the bacterial community composition and associated residue-N mineralization from the rhizosphere to the bulk soil will advance our knowledge of root-mediated residue-N transformation in agroecosystems.

In order to examine the role of microbes in mineralization of N from different crop residues, we conducted an experiment using a rhizobox system (experimental mesocosm that allows to separate rhizosphere and bulk soil) (Youssef and Chino 1988; Jin et al. 2022) and ^{15}N-labelled soybean and maize residues, and investigated the microbiome associated with the residue-N mineralization in the rhizosphere. We hypothesized that the residue-N mineralization would be stronger in the rhizosphere compared to the bulk soil because rhizodeposits could increase microbial biomass size and activity, and change the bacterial community composition in the rhizosphere. This change could indicate the stimulation of microbial metabolic activity that is responsible for the enhanced decomposition of crop residues in the rhizosphere and

consequent release of N from the residues. Moreover, the microbial community associated with residue-N mineralization in the rhizosphere might vary between residues differing in C/N ratio.

Materials and methods

Rhizobox construction

The rhizobox was made of PVC sheet with the dimension of 20 cm × 12 cm × 20 cm (length × width × height) (Fig. S1) (Youssef and Chino 1988). It consisted of a central compartment (6 mm in width with 165 g soil) designed for soybean root growth, and 0 − 2 mm and 2 − 4 mm compartments (2 mm in width for each compartment with 55 g soil) adjoining each side of the central compartment. U-shape plastic frames covered with nylon mesh (< 25 μm) were used to separate these compartments, i.e. between the central and 0 − 2 mm compartments, between 0 − 2 and 2 − 4 mm compartments, and between 2 − 4 mm compartment and bulk soil (> 4 mm). This mesh size does not allow roots to penetrate but allows free movement of soil solution and microorganisms. We defined the root, 0 − 2 mm and 2 − 4 mm compartments as central, proximal and transitional rhizosphere zones, respectively. The soil outside these compartments (> 4 mm from the central compartment) was treated as bulk soil. With a rhizobox, the soils from various zones could be precisely collected and the effectiveness of the rhizosphere effect on the microbes and residue-N mineralization could also be spatially assessed because root exudates/rhizodeposits form a gradient along compartments towards the bulk soil.

^{15}N labeling of crop residues

Soybean and maize plants used for ^{15}N-labelling were grown in a Mollisol soil that had an organic C content of 28 g kg^{-1} dry weight soil, total N of 2.2 g kg^{-1} dry weight soil, available N of 160 mg kg^{-1} dry weight soil, and a pH of 5.4 (1:5 H_2O). Soil available N (NH_4^+ and NO_3^-) was determined by the alkaline hydrolysis method (Cornfield 1960). $Ca(NO_3)_2$ containing 20% of ^{15}N atom excess was added at 100 mg N kg^{-1} dry weight soil and was homogenized with the soil before sowing.

Uniformly-sized seeds were germinated on moistened filter paper at 25 °C in the dark for 24 h. Six germinated seeds were sown in each pot (20 cm diameter and 40 cm high) containing 9.5 kg dry weight soil, and thinned to 3 plants for soybean and 1 plant for maize after emergence. Soil water content was maintained at 80 ± 5% of field capacity by weighing and watering.

Plants were harvested at maturity, 130 days after sowing, dried at 70 °C, and ground through a 2-mm sieve. Then, the ground materials were sieved to exclude particle sizes of < 0.25 mm. The residues with size ranging from 0.25 to 2.00 mm were used for the rhizobox experiment to ensure a precise treatment effect. The concentrations of total C and N were 477 and 9.3 g kg^{-1} for soybean residue (C/N = 51.3), and 431 and 4.1 g kg^{-1} for maize residue (C/N = 105), respectively. The soybean and maize residues had 5.01% and 9.15% of ^{15}N atom-excess, respectively.

Experimental design and plant growth

The experiment had three residue treatments in three replicates, 1) maize residue, 2) soybean residue and 3) no-residue control. In order to compare the mineralization of residue-N between the residue treatments, the particle size of residues was 0.25–2.00 mm, the calculated amount of residues was homogenized with the soil in each compartment to give an equal amount of N input of 10.3 mg N kg^{-1} dry weight soil. The application rate of maize residue was 2.50 g kg^{-1} dry weight soil and of the soybean residue was 1.11 g kg^{-1} dry weight soil, which are equivalent to 8 and 3.6 t ha^{-1} for maize and soybean residues, respectively, representing maize and soybean residue amendments typical for the region (Xie et al. 2021).

The Mollisol was sampled from a field without fertilization for five years at Guangrong Village (47°23'N, 126°51'E) and was air-dried and sieved through a 2-mm sieve. The soil was a silty clay (sand 19%, silt 44% and clay 37%). It had a pH of 6.9 (1:1 w/v in H_2O), an organic C content of 25 g kg^{-1} dry weight soil, total N, P and K of 1.9, 0.73 and 20 g kg^{-1} dry weight soil, respectively, and soil available N (NH_4^+ and NO_3^-), Olsen P (Olsen et al. 1954) and available K of 75, 43 and 130 mg kg^{-1} dry weight soil, respectively.

Soybean plants were grown in soybean- or maize-residue-amended soils. The cultivar used in this study was Dongsheng 1, widely grown in Northeast

China. Soybean seeds were germinated in sterilized sand at 28 °C for 2 days, then three uniform seedlings were transplanted to the central compartment of each rhizobox. The plants grew in a glasshouse at 22 − 26 °C during the day and 18 − 22 °C at night. During the growth period, the soil water content was maintained at about 80 ± 5% of field capacity.

Sampling and soil physicochemical analyses

Plants were harvested 55 days after sowing. Soil in each compartment was collected separately. In each rhizobox, soils from two-side compartments with the same distance from the central compartment were combined and well mixed. Approximately 2 g of soil from each of four samples, i.e. the central, 0 − 2 mm and 2 − 4 mm compartments and the bulk soil, per rhizobox was stored at -80 °C for DNA extraction. The remaining soil was analyzed for chemical and biochemical properties.

Soil pH was measured using a pH meter after mixing soil in water (1:5 w/v) for 30 min. Soil available N (NH_4^+ and NO_3^-) was extracted from 5 g moist soils with 100 mL of 1 M KCl, and its concentrations were measured using a flow-injection auto-analyser (SKALAR, San + +, Netherlands) (Rayment and Lyons 2011). Olsen P was extracted from 2 g air-dried soil in 50 ml of 0.5 M $NaHCO_3$ (Olsen et al. 1954) and analyzed colorimetrically (Murphy and Riley 1962). The concentration of total soil N was determined using an elemental analyzer (Elementar Analysensysteme, Hanau, Germany). Air-dried soil and oven-dried residues were ground with a ball mill (Retsch MM400, Hanau, Germany) before ^{15}N atom % of the samples was measured with an isotope ratio mass spectrometer (Deltaplus, Finnigan MAT, Bremen, Germany). Microbial biomass C (MBC) was quantified using the fumigation extraction method (Vance et al. 1987; Wu et al. 1990). Briefly, 10 g of moist soil was fumigated with $CHCl_3$ in a vacuum desiccator followed by immediate extraction with 40 mL of 0.5 M K_2SO_4, and measurement of total extractable C released by $CHCl_3$ using an automated TOC analyzer (Shimadzu, TOC-VCPH, Japan). Changes in extractable C due to fumigation were used to calculate microbial biomass C ($k_{EC} = 0.37$) (Joergensen 1996). The extractable C in the non-fumigated soil was considered as dissolved organic C (DOC) (Domanski et al. 2001). Regarding the measurement of soil respiration, 10 g of each fresh soil sample was incubated at 25 °C for 24 h in a 0.25-L air-tight Mason jar with 10 mL of 1.0 M NaOH in a vial placed in it to trap the evolved CO_2. The CO_2 trapped in the NaOH solution was precipitated with a 1.0 M $BaCl_2$ solution, and the solution was then titrated with 0.5 M HCl against a phenolphthalein indicator (Blagodatskaya et al. 2011).

DNA extraction and Illumina MiSeq sequencing

Soil DNA was extracted from 0.5 g fresh soil using a Fast DNA SPIN Kit for Soil (Qbiogene Inc. Carlsbad, CA, USA). The DNA concentration was determined using NanoDrop 2000 (Thermo Scientific, Waltham, MA, USA) and then the DNA samples were stored at -20 °C until further analyses.

Regarding MiSeq sequencing, the V3 − V4 region of the prokaryotic 16S rRNA gene was amplified using primers 338-F (5′- ACTCCTACGGGAGGC AGCAG-3′) and 806-R (5′- GGACTACHVGGG TWTCTAAT-3′) with 7-bp unique barcodes at the 5′ end. The PCR program was described as an initial denaturation at 94 °C for 3 min, followed by 30 cycles of 94 °C for 40 s, 56 °C for 60 s, and 72 °C for 60 s, and a final extension at 72 °C for 10 min. Two biological replicates for each sample were conducted in PCR reactions to minimize PCR bias, and PCR products of the two replicates were combined. The sequencing library was prepared by pooling the amplicons from all samples with an equimolar concentration. The high throughput sequencing was performed on an Illumina MiSeq PE 300 platform at Majorbio BioPharm Technology Co., Ltd., Shanghai, China.

After sequencing, adapters were trimmed with the qiime cutadapt trim-paired tool (Martin 2011). Sequence pairs were merged using FLASH software. Regarding quality control of sequencing, we processed primer trimming, denoising and chimera removal, followed by assigned amplicon sequence variants using DADA2 algorithm in QIIME2 (Bolyen et al. 2019; Callahan et al. 2016). The taxonomic assignment of ASVs was carried out by a Naive Bayes classifier against the SILVA database (release 138) for bacteria (Quast et al. 2012). In total, 893,912 high-quality sequences were obtained with a range of 18,898 to 31,494 sequences for individual samples. To minimize the impact of sequence count variation

among samples, a random subset of 18,898 sequences was selected based on the minimum number of sequences across samples, representing 5932 ASVs. The raw sequences were deposited in the NCBI short-read archive PRJNA679167.

Calculations and data analyses

The decomposed proportion of ^{15}N-labelled maize and soybean residues (DPN_r) was given by Robinson (2001) and Wang et al. (2019a, b):

$$DPNr = 100 - h \times \left[\left(\delta^{15}N_{sample} - \delta^{15}N_{soil}\right)/\left(\delta^{15}N_{residue} - \delta^{15}N_{soil}\right)\right] \times 100/g$$

where $\delta^{15}N_{sample}$ is the $\delta^{15}N$ value of soil samples with residue addition; $\delta^{15}N_{soil}$ is the $\delta^{15}N$ value of soil without residue addition, and $\delta^{15}N_{residue}$ is the $\delta^{15}N$ value of the maize or soybean residue; h is the total soil N content; g is the N content of ^{15}N-labelled maize or soybean residue. In this study, we considered the loss of residue-N as residue-N mineralization.

$$\text{Residue N mineralization} = g \times DPN_r$$

The N-mineralization-associated taxa at the ASV level were obtained by identifying the total 5932 rarefied ASVs that exhibited significant positive correlations with the proportion of mineralized N across the rhizosphere compartments (from rhizosphere to bulk soil) (Spearman, $p < 0.05$), using SPSS software (version 19.0). Thus, the rhizosphere effect on N-mineralization-associated taxa could be assessed. Moreover, random forest (RF) modeling was performed to assess variables that might covary with N mineralization, and showed that the N mineralization of crop residue had the highest value of IncMSE (> 10%) in RF regulating the N-mineralization-associated bacterial community structure, followed by the concentrations of dissolved organic C and NO_3^--N in soil. In order to avoid the false positive problem in the multiple significance tests, we used the false discovery rate (FDR = 0.05) approach to adjust p values to q values. Repeated measures ANOVA was used to reveal the residue (as the main plot) and compartment effects (compartment as subplot) on N mineralization, alpha-diversity and microbial respiration. The relationships between the relative abundance of bacterial taxa or alpha-diversity and the soil factors were determined using Pearson correlation at the adjusted $p < 0.05$. In addition, the relative abundances of N-mineralization-associated taxa was the total relative abundance of all N-mineralization-associated taxa under the maize and soybean residue amendments. Based on the Bray–Curtis distance at the ASV level, the non-metric multidimensional scaling (NMDS) analysis and redundancy analysis (RDA) were performed using the 'vegan' in R platform (version 3.2.5) (R Development Core Team 2016). Moreover, the permutational multivariate analysis of variance (PERMANOVA) and analysis of similarities (ANOSIM) were performed to statistically assess the difference in the microbial community composition between treatments.

Functional profiling of N-mineralization-associated bacterial taxa was performed using the PICRUSt2 algorithm. PICRUSt2 is the most flexible and accurate way to predict the functional profiles of microbial communities based on their taxonomic composition. The major concern of this approach is that amplicon-based predictions cannot provide strain-specific functionality (Douglas et al. 2020). Thus, more robust methodology, such as metagenomic analysis, is recommended in the future. Kyoto Encyclopedia of Genes and Genomes (KEGG) module and pathway composition were generated according to the assignment of KEGG Orthologies (Kos) at https://www.kegg.jp/. Targeted Kos of marker genes involved in C and N metabolic pathways were extracted as a subject database (Table S1). A Z-score transformation was applied to the reads before statistical analyses.

Results

Residue-N mineralization in the rhizosphere

The proportion of the N mineralized from crop residue significantly decreased from 26% in the central compartment to 18% in the bulk soil amended with the soybean residue and from 24 to 12% in the maize residue treatment (Fig. 1). The proportion of N mineralized from the soybean residue was significantly higher than that from the maize residue in the central and 2 – 4 mm (transitional) compartments. The total mineralized

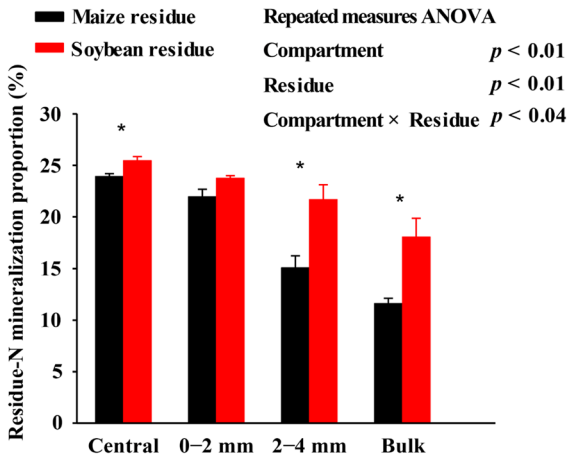

Fig. 1 The proportion of N mineralized from maize and soybean residues in the central, 0 – 2 mm (approximal), 2 – 4 mm (transition) and > 4 mm (bulk soil) compartments. Asterisks (*) denote significant differences between residue amendments at $p < 0.05$. Error bars represent the standard error of three replicates

residue-N was 0.40 – 0.44 mg per rhizobox in the central compartment and 0.07 – 0.13 mg in the 2 – 4 mm (transitional) compartment, and soybean residue had 12.6% more N mineralized than maize residue across the compartments (Fig. S2).

Soil biochemical properties and plant biomass

Soil chemical properties varied with distance from the plant roots and between the residues. The mean concentrations of Olsen P, NH_4^+-N and NO_3^--N in the central compartment were 8.73, 138 and 19.4 mg kg^{-1} dry weight soil, respectively, which were significantly lower than those in the bulk soil. Soil pH, DOC and MBC had the opposite trend, being 5.82, 189 and 366 mg kg^{-1} dry weight soil in the central compartment, 0.16 units, 35% and 31% higher than those in the bulk soil, respectively (Table S2). Both residue amendments significantly increased the concentrations of NH_4^+-N and MBC across rhizobox compartments (central, proximal and transitional compartments) by 28 – 31% and 63 – 68% compared to the control, respectively. The amendment of maize but not soybean residue, significantly reduced NO_3^--N concentration in the central, 0 – 2 (proximal) and 2 – 4 mm (transitional) compartments compared to the control. Residue amendment did not change SOC concentrations (Table S2). Soil respiration rate in the 0 – 4 mm (proximal and transitional) compartments was 71 – 109% higher than that in the bulk soil, with the effect being the greatest with soybean residue, and least in the control (Fig. S3).

Plant shoot dry biomass was 3.9 and 4.0 g $plant^{-1}$ for the maize and soybean residue treatments, respectively, which was 5% higher than that of the control. It was significantly higher for the soybean (but not maize) residue treatment compared to the control (Fig. S4). Both residue amendments resulted in significantly greater root biomass than the control.

Alpha-diversity of bacterial community

The rarefaction coverage was above 99% for all of the samples. The ANOVA showed that bacterial alpha-diversity was significantly lower in the rhizosphere compared to the bulk soil (Table 1). In particular, sobs, Ace, Chao1 and Shannon were 14%, 13%, 14% and 4% lower in the central compartment than in the bulk soil, respectively.

The Pearson's correlation analyses showed that the Ace index was correlated negatively with soil pH, but positively with the concentrations of Olsen P and soil available N (Table S3). Shannon index was correlated negatively with soil pH and DOC, but positively with the concentrations of Olsen P and available N. These diversity parameters did not correlate with MBC or respiration rate.

Beta-diversity of bacterial community

Actinobacteriota, Proteobacteria, Acidobacteriota and Chloroflexi were the four most abundant phyla, accounting for 19–34%, 18–34%, 11–25%, and 4.6–12% of the total sequences, respectively (Fig. 2a). The NMDS plot showed that bacterial community composition gradually shifted from the central compartment to the bulk soil, i.e. in the order of the central, 0–2 (proximal) and 2–4 mm (transitional) compartments and bulk soil. The PERMANOVA and ANOSIM analysis indicate that residue amendment significantly affected the whole bacterial community composition only in the bulk soil ($p < 0.05$), but not in the rhizosphere compartments ($p > 0.05$) (Fig. 2b, Table S4).

The RDA revealed strong associations ($p < 0.05$) of the bacterial community composition with soil pH and the concentrations of dissolved organic C, NO_3^--N, NH_4^+-N and Olsen P (Fig. S5).

Table 1 Microbial diversity, as estimated by three indices of species richness [observed ASVs (sobs) and estimated richness from ASV abundance (Chao1, ACE)] and one index of within-sample ASV diversity (Shannon) in soils of various rhizobox compartments (central, 0–2 mm, 2–4 mm and > 4 mm) without (Control) or with maize and soybean residues to the central compartment. Repeated measures ANOVA was performed to demonstrate the effects of compartment and residue, and their interactions on variables. Lower-case letters are the posthoc results and means followed by different letters indicate significant difference within a column at $p \leq 0.05$ (LSD)

Rhizobox compartments	Residue treatments	Sobs	Shannon	Ace	Chao1
Central	Control	1048 d	6.45 cd	1052 d	1051 d
	Maize	1031 d	6.38 d	1034 d	1034 d
	Soybean	1182 bcd	6.51 cd	1191 bcd	1193 bcd
0 – 2 mm	Control	1022 d	6.51 cd	1024 d	1023 d
	Maize	1133 cd	6.61 abc	1138 cd	1138 cd
	Soybean	1243 abc	6.68 ab	1251 abc	1251 abc
2 – 4 mm	Control	1044 d	6.52 bcd	1045 d	1044 d
	Maize	1283 abc	6.70 a	1292 abc	1291 abc
	Soybean	1287 abc	6.68 ab	1299 abc	1301 abc
Bulk (> 4 mm)	Control	1186 bcd	6.61 abc	1189 bcd	1188 bcd
	Maize	1315 ab	6.70 a	1324 ab	1323 ab
	Soybean	1395 a	6.74 a	1408 a	1407 a
Significance level	Compartment	< 0.01	< 0.01	< 0.01	< 0.01
	Residue	< 0.01	0.03	< 0.01	< 0.01
	Compart × residue	0.46	0.52	0.47	0.47

Rhizobacterial taxa associated with residue N mineralization

The bacterial taxa, 93 ASVs in total, that were positively correlated in relative abundance with the proportion of N mineralized from the residue ($q < 0.05$) were considered as N-mineralization-associated bacterial taxa in the rhizosphere (Table S5). Random forest (RF) modeling was performed to identify the key indicators that drive the N-mineralization-associated bacterial community structures, we found that the proportion of the N mineralized from crop residue played the most important role with the highest value of IncMSE (> 10%) for RF, regulating the N-mineralization-associated bacterial community structures (Fig. S6). Those bacterial taxa were considered to be functionally involved in N mineralization, which was further verified in PICRUSt2. The total relative abundances of N-mineralization-associated taxa were significantly higher in the rhizosphere than in the bulk soil (Fig. 3a). In order to compare the overall potential microbial capability of mineralizing N between soybean and maize residues, the total relative abundances of N-mineralization-associated taxa in the rhizosphere were correlated with proportions of mineralized N. The coefficient of the linear correlation for the soybean residue treatment was significantly higher than for the maize residue treatment, indicating more enrichment of microbial taxa for the unit of residue-N mineralization (Fig. 3b, c).

The NMDS analysis revealed that the amendment of soybean and maize residues resulted in distinct clusters of the bacterial community with significant ($q < 0.05$) differences in taxonomy (Fig. 4a; Table S5). In the central compartment, maize residue resulted in significantly higher relative abundances of the N-mineralization-associated genera *Paraburkholderia*, *Ralstonia*, *Kutzneria* and *Edaphobaculum* than soybean residue while the opposite was true for *Streptomyces, Kribbella* and *Microbacterium* (Fig. 5).

The RDA revealed strong relationships ($p < 0.05$) between the composition of the residue-N mineralization-associated bacterial community and soil pH and the concentrations of dissolved organic C, NO_3^--N and Olsen P (Fig. 4b; Table S6). The PERMANOVA analysis indicated that the composition of the N-mineralization-associated bacterial community was mainly shaped by the chemical properties of the rhizosphere (Fig. 4c), which accounted for 43.8% of the variation in the composition of the

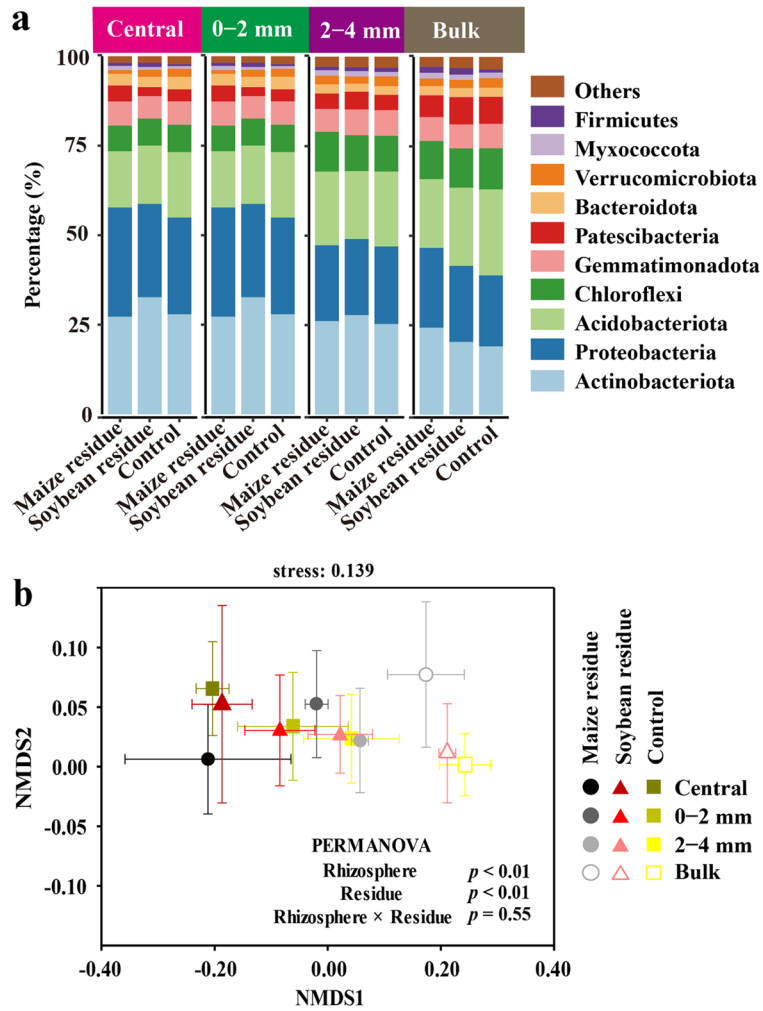

Fig. 2 Relative abundances of the dominant bacterial phyla (**a**) and nonmetric multidimensional scaling (NMDS) plot based on the Bray–Curtis distance with significant indications of PERMANOVA (**b**) in the central, 0 – 2 mm (proximal) and 2 – 4 mm (transitional) compartments and the bulk soil (> 4 mm) under the maize residue, soybean residue and no-residue control. Error bars represent the standard error of three replicates

N-mineralization-associated bacterial community in comparison to 5.56% due to the residue type.

At the metabolic level, the soybean residue amendment significantly increased the predicted abundance of major ammonification genes encoding urease, glutamate dehydrogenase and glutaminase, and C-decomposition genes encoding cellulase and chitinase compared to the maize residue amendment (Fig. S7). Moreover, the predicted abundances of those genes were positively correlated with mineralized N (Table S7).

Discussion

This study showed that the residue-N mineralization was greater in the rhizosphere zones than the bulk soil (Fig. 1). The higher concentrations of dissolved organic C and microbial biomass C, and respiration rate in the rhizosphere zones than the bulk soil (Table S2, Fig. S3) indicate that plants released organic C compounds into the rhizosphere and supported microbial growth (Deng et al. 2022; He et al. 2020; Marschner and Kalbitz 2003), thus leading to an increase in residue decomposition and N mineralization as a result of a rhizosphere priming effect (RPE) (Cheng and Kuzyakov 2005; Xu et al. 2019; Yu et al. 2018). Furthermore, our study demonstrated that the soil in direct proximity to plant roots had decreased available N compared to the bulk soil (Table S2), which would stimulate the secretion of enzymes by microbes to decompose organic materials in the soil, so as to meet their N requirement (Fontaine et al. 2011; Lu et al. 2019). Interestingly, the soybean residue exhibited a higher proportion

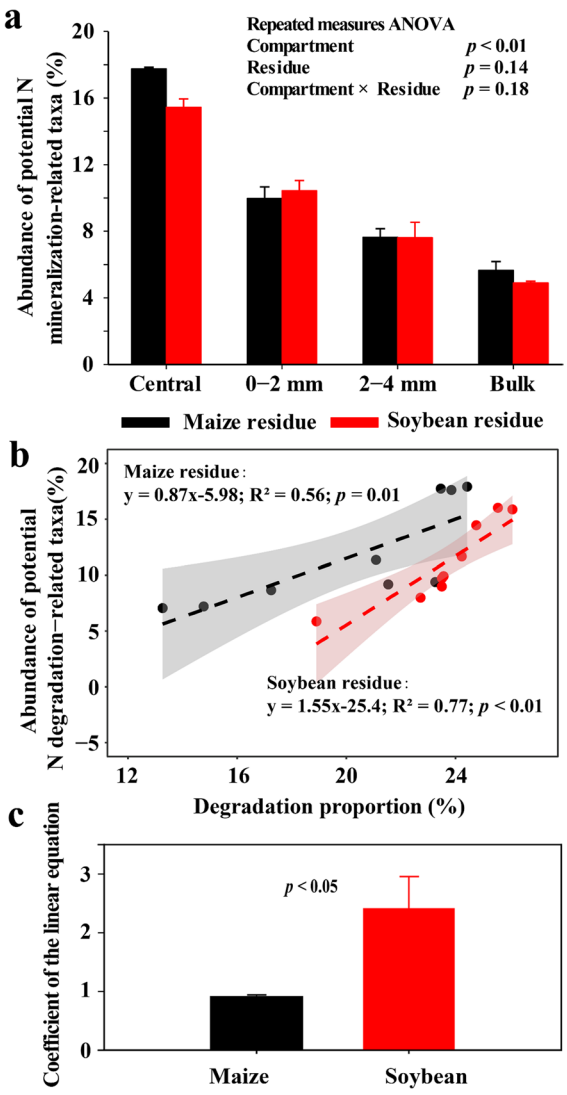

Fig. 3 The sum of relative abundances of N-mineralization-associated taxa in the central, 0−2 mm (proximal) and 2−4 mm (transitional) and > 4 mm (bulk soil) compartments under maize and soybean residue amendments (**a**), the relationships between the sum of relative abundances of N-mineralization-associated taxa and residue-N mineralization proportion from rhizosphere to bulk soil (**b**) and the coefficients of the respective correlation equations (**c**). Error bars represent the standard error of three replicates

of N mineralization in the rhizosphere zones than the maize residue (Fig. 1), indicating that the microbial accessibility to residue N depended on the residue type (or residue C/N ratio) and the interaction with the rhizosphere priming effect on the shift of the microbial community composition (Abiven et al. 2011; Zhang et al. 2008). Due to the greater C/N ratio of the residues than microorganisms, the process of residue decomposition is dominantly N-limited (Henriksen and Breland 1999). The greater predicted abundance of N-mineralization and organic C-decomposition genes in the rhizosphere amended with soybean residue than with maize residue (Fig. S7) further demonstrated microbial functional preference on the N mineralization of residues with a low C/N ratio.

The rhizosphere ($R^2 = 0.64$) had a stronger effect (43.8%) than residue type (5.56%; Fig. 4c) on the composition of bacterial community involved in the mineralization of residue N. The increasing demand of microbial N due to the high pH and low available N and dissolved organic C concentrations in the rhizosphere zones (Table S2) shaped bacterial community favoring the stimulation of residue-N mineralization. This is supported by the significant association of these two parameters with the relative abundances of residue-N-mineralization-associated taxa (Fig. 4b). Moreover, those parameters were also significantly associated with the composition of the whole community (Fig. S5), indicating that the N-mineralizing community corresponded with the whole community in response to soil N/C chemical properties.

Among the community in the central zone, *Paraburkholderia* and *Ralstonia* were associated with N mineralization of the maize residue whereas *Streptomyces* and *Kribbella* were associated with the mineralization of the soybean residue. *Paraburkholderia* are root-nodulating bacteria (Zwetsloot et al. 2020). They can utilize labile organic C exuded into the rhizosphere by the host plant under the low-N availability (Belova et al. 2006; Su et al. 2020; Weisskopf et al. 2011), and also degrade recalcitrant C compounds, such as benzoate and betaine (Weber and King 2017). However, it remains unknown whether these bacterial taxa mineralize residue N as the result of residue-C degradation or whether they form a symbiosis with soybean roots, given the likely proliferation of N-fixing microbes under low-N availability (Bao et al. 2019, 2020).

Streptomyces were dominant during the mineralization of soybean residue (Espana et al. 2011; Wang et al. 2019a, b; Lian et al. 2019). *Kribbella* have been found to utilize various organic N sources such as glutamine, proline, serine and threonine (Albuquerque et al. 2011; Zhao et al. 2019). These results indicate that the shift in the composition of the

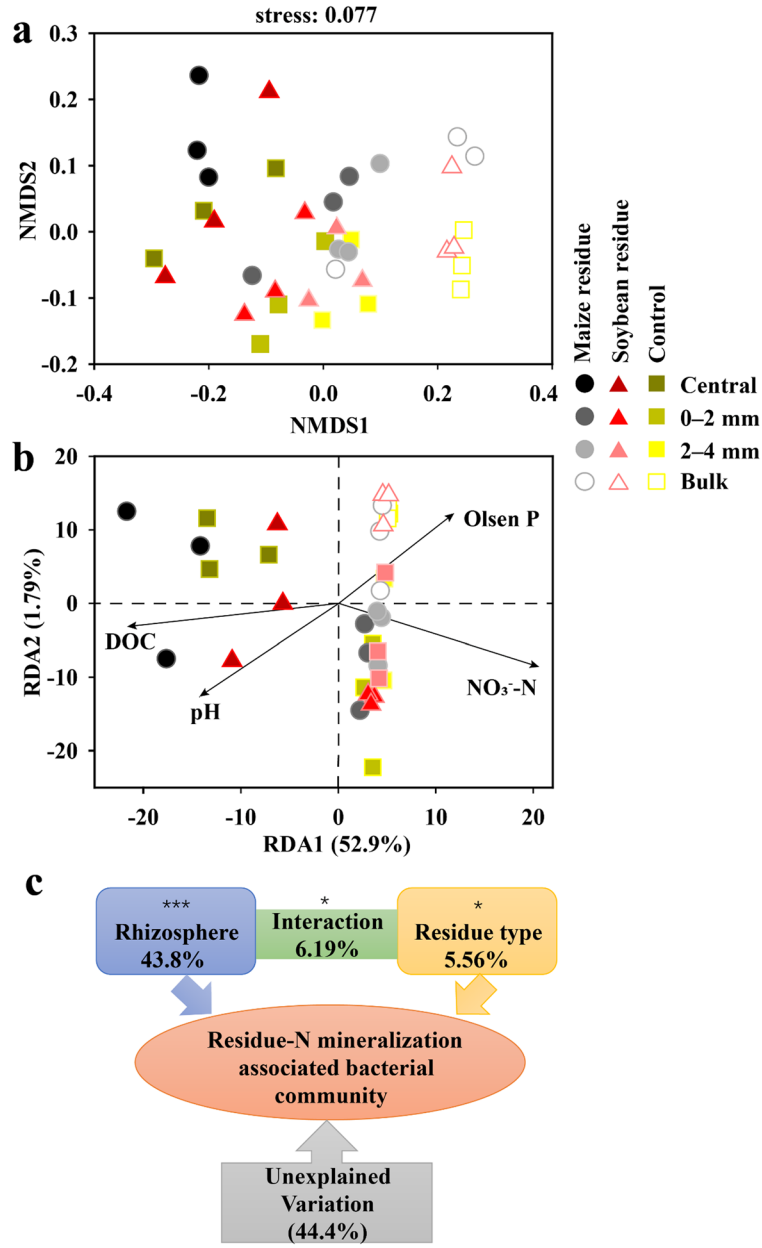

Fig. 4 Nonmetric multidimensional scaling (NMDS) analysis of residue-N mineralization-related taxa based on the Bray–Curtis distance (**a**), redundancy analysis (RDA) demonstrating the relationships between soil environmental variables and residue-N mineralization-associated taxa (**b**), and variation partition analysis of the effects of rhizosphere and residue type on the composition of residue-N mineralization-related community with permutational multivariate analysis of variance (PERMANOVA) (**c**). Asterisks * and *** denote significant differences at $p < 0.05$ and $p < 0.001$, respectively. DOC represents dissolved organic C

microbial community in the rhizosphere of soybean potentially drove the residue-N mineralization. Furthermore, the greater microbial activity in response to the soybean compared to the maize residue amendment in the rhizosphere (Fig. S3) indicates that the rhizobacterial community might metabolically accelerate the process of residue-N mineralization, especially for the soybean residue. It appears that the C/N ratio in the residue might strongly contribute to the specific change of bacterial taxa associated with residue-N mineralization though other constituents of residue, such as lignin to some extent, shift the bacterial community composition as well (Wang et al. 2019a, b). Furthermore, the increased abundances of the N- and C-metabolizing genes in the rhizosphere, especially under residue amendment (Fig. S6), reflect the increased functional potential within the microbial community to mineralize residue-N.

The greater N mineralization from soybean residue than maize residue was attributed to the greater microbial activity and respiration in the rhizosphere amended

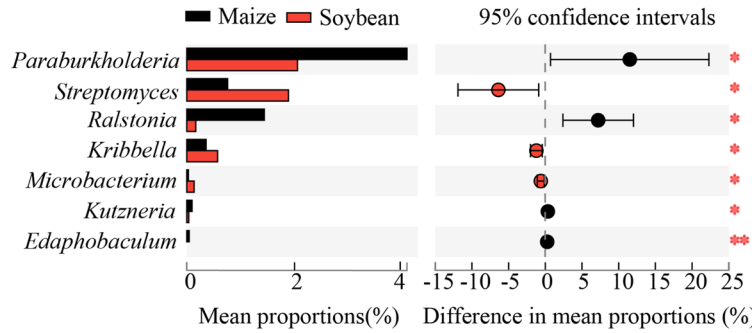

Fig. 5 The significant differences between maize and soybean residue amendments in the relative abundance of residue-N mineralization-associated genera in the central compartment of the rhizoboxes. Error bars represent the standard error of three replicates

with soybean residue (Fig. S3). It was also related to the greater relative abundance of the N-mineralization-associated taxa against the unit of mineralized reside-N mineralization (Fig. 3b, c). The significant increase in the major predicted ammonification genes (Fig. S7) in the soybean residue treatment further supported this observation. Although its concentrations in the rhizosphere zones were greater under soybean residue than maize residue amendment, NO_3^--N accounted for less than 10% of total mineral N, which would not suppress microbial mineralization of soybean residue N. However, the functional contribution of those specific microbial members to the mineralization of soybean residue-N needs to be quantified.

Our results imply that, in farming systems, the rhizosphere effect is likely to boost microbial C- and N-metabolizing functions to accelerate the residue decomposition, especially for soybean residues, highlighting that subsequent crops alter the residue-N cycling belowground via rhizosphere priming effect, and access nutrient resources. This rhizosphere effect on the residue decomposition should be considered in nutrient management with crop residue amendment.

The effect of rhizosphere properties overwhelmed the impact of residue type on the bacterial community composition (PERMANOVA, $p < 0.05$) (Fig. 2b). Root exudates and rhizodeposits exert the dominant influence on microbial colonization in the rhizosphere (Dennis et al. 2010), and stimulate microbial activities and metabolic processes (He et al. 2020; McCormack et al. 2017; Xu et al. 2019). In addition, low N availability in the rhizosphere due to plant uptake may also structure the microbial community (Jin et al. 2022). The gradient of the rhizodeposits and chemical properties results in the gradual shift of microbial community across the rhizosphere. Previous studies indicated that the distance to the root surface defines the composition of the bacterial community (Edwards et al. 2015; Sasse et al. 2018). However, Edwards et al. (2015) found that organic material input significantly altered the microbial community composition in the rice rhizosphere under field conditions. The different findings between the studies could be attributed to the difference in sampling precision. The rhizobox device used in this study allowed us to examine spatial variations of the rhizosphere in controlled-environment conditions and enabled the precise collection of rhizosphere soil (Sasse et al. 2018). However, the limited space of the rhizobox device might constrain root growth and residue mineralization.

Conclusions

The residue-N mineralization was accelerated in the rhizosphere where the amount of N mineralized from the soybean residue was greater than that from the maize residue. The increase of dissolved organic C and depletion of available N in the rhizosphere of soybean was accompanied by the recruitment of bacterial taxa that were associated with residue-N mineralization. However, the efficacy of the dominant microbiome in the residue-N mineralization in the rhizosphere requires further investigation on N-related metabolic pathways with the advancement of metagenomic sequencing techniques.

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Data availability Datasets generated and/or analysed in the current study are available from the corresponding author on reasonable request.

References

Abera Y, Masso C, Assefa F (2019) Inoculation with indigenous rhizobial isolates enhanced nodulation, growth, yield and protein content of soybean (*Glycine max* L.) at different agro-climatic regions in Ethiopia. J Plant Nutr 42:1900–1912

Abiven S, Heim A, Schmidt MWI (2011) Lignin content and chemical characteristics in maize and wheat vary between plant organs and growth stages: consequences for assessing lignin dynamics in soil. Plant Soil 343:369–378

Albuquerque L, Franca L, Rainey FA, Schumann P, Nobre MF, da Costa MS (2011) *Gaiella occulta* gen. nov. sp. nov. a novel representative of a deep branching phylogenetic lineage within the class *Actinobacteria* and proposal of *Gaiellaceae* fam. nov. and *Gaiellales* ord. nov. Syst Appl Microbiol 34:595–599

Bao Y, Dolfing J, Wang B, Chen RR, Huang MS, Li ZP, Lin XG, Feng YZ (2019) Bacterial communities involved directly or indirectly in the anaerobic degradation of cellulose. Biol Fertil Soils 55:201–211

Bao Y, Guo Z, Chen RR, Wu M, Li ZP, Lin XG, Feng YZ (2020) Functional community composition has less environmental variability than taxonomic composition in straw-degrading bacteria. Biol Fertil Soils 56:869–874

Belova SE, Pankratov TA, Dedysh SN (2006) Bacteria of the genus *Burkholderia* as a typical component of the microbial community of *Sphagnum* peat bogs. Microbiology 75:90–96

Bird JA, Herman DJ, Firestone MK (2011) Rhizosphere priming of soil organic matter by bacterial groups in a grassland soil. Soil Biol Biochem 43:718–725

Blagodatskaya E, Yuyukina T, Blagodatsky S, Kuzyakov Y (2011) Turnover of soil organic matter and of microbial biomass under C_3–C_4 vegetation change: Consideration of ^{13}C fractionation and preferential substrate utilization. Soil Biol Biochem 43:159–166

Bolyen E, Rideout JR, Dillon MR, Bokulich NA, Abnet CC, Al-Ghalith GA, Alexander H (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat Biotechnol 37:852–857

Burgess MS, Mehuys GR, Madramootoo CA (2002) Nitrogen dynamics of decomposing corn residue components under three tillage systems. Soil Sci Soc Am J 66:1350–1358

Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP (2016) DADA2: high-resolution sample inference from Illumina amplicon data. Nat Methods 13:581–583

Castanha C, Zhu B, Pries CEH, Georgiou K, Torn MS (2018) The effects of heating, rhizosphere, and depth on root litter decomposition are mediated by soil moisture. Biogeochemistry 137:267–279

Cheng W, Kuzyakov Y (2005) Root effects on soil organic matter decomposition. In: Zobel RW, Wright SF (eds) Roots and soil management: interactions between roots and the soil. Agronomy Monograph No. 48. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, USA, 119–143

Cornfield AH (1960) Ammonia released on treating soils with N-sodium hydroxide as a possible means of predicting the nitrogen-supplying power of soils. Nature 187:260–261

Deng J, Deng Y, Sun Z (2022) Tillage and residue management affect growing-season soil respiration in paddy fields. Soil Till Res 218:105315

Dennis PG, Miller AJ, Hirsch PR (2010) Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiol Ecol 72:313–327

Ding W, Li S, He P, Huang S (2019) Contribution and fate of maize residue-^{15}N and urea-^{15}N as affected by N fertilization regime. Plos One 14: e0210176

Domanski G, Kuzyakov Y, Siniakina SV, Stahr K (2001) Carbon flows in the rhizosphere of ryegrass (*Lolium perenne*). J Plant Nutr Soil Sci 164:381–387

Douglas GM, Maffei VJ, Zaneveld JR, Yurgel SN, Brown JR, Taylor CM, Huttenhower C, Langille MGI (2020) PICRUSt2 for prediction of metagenome functions. Nat Biotechnol 38:685–688

Edwards J, Johnson C, Santos-Medellín C, Lurie E, Podishetty NK, Bhatnagar S, Eisen JA, Sundaresan V (2015) Structure, variation, and assembly of the root-associated microbiomes of rice. Proc Natl Acad Sci USA 112:e911–e920

Espana M, Rasche F, Kandeler E, Brune T, Rodriguez B, Bending GD, Cadisch G (2011) Identification of active bacteria involved in decomposition of complex maize and soybean residues in a tropical Vertisol using ^{15}N-DNA stable isotope probing. Pedobiologia 54:187–193

Fontaine S, Henault C, Aamor A, Bdioui N, Bloor JMG, Maire V, Mary B, Revaillot S, Maron PA (2011) Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. Soil Biol Biochem 43:86–96

Hall SJ, Russell AE, Moore AR (2019) Do corn-soybean rotations enhance decomposition of soil organic matter? Plant Soil 444:427–442

He YH, Cheng WX, Zhou LY, Shao JJ, Liu HY, Zhou HM, Zhu K, Zhou XH (2020) Soil DOC release and aggregate disruption mediate rhizosphere priming effect on soil C decomposition. Soil Biol Biochem 144:107787

Henriksen TM, Breland TA (1999) Evaluation of criteria for describing crop residue degradability in a model of carbon and nitrogen turnover in soil. Soil Biol Biochem 31:1135–1149

Hu GQ, Liu X, He HB, Zhang W, Xie HT, Wu YY, Cui JH, Sun C, Zhang XD (2015) Multi-seasonal nitrogen recoveries from crop residue in soil and crop in a temperate agro-ecosystem. PLoS One 10:e0133437

Huo C, Luo Y, Cheng W (2017) Rhizosphere priming effect: a meta-analysis. Soil Biol Biochem 111:78–84

Jin J, Krohn C, Franks AE, Wang XJ, Wood JL, Petrovski S, McCaskill M, Batinovic S, Xie ZH, Tang CX (2022) Elevated atmospheric CO_2 alters the microbial community composition and metabolic potential to mineralize organic phosphorus in the rhizosphere of wheat. Microbiome 10:12

Joergensen RG (1996) The fumigation-extraction method to estimate soil microbial biomass: calibration of the k_{EC} value. Soil Biol Biochem 28:25–31

Knorr M, Frey SD, Curtis PS (2005) Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86:3252–3257

Li DD, Li ZQ, Zhao BZ, Zhang JB (2020) Relationship between the chemical structure of straw and composition of main microbial groups during the decomposition of wheat and maize straws as affected by soil texture. Biol Fertil Soils 56:11–24

Li YS, Yu ZH, Liu XB, Mathesius U, Wang GH, Tang CX, Wu JJ, Liu JD, Zhang SQ, Jin J (2017) Elevated CO_2 increases nitrogen fixation at the reproductive phase contributing to various yield responses of soybean cultivars. Front Plant Sci 8:1546

Li ZQ, Zhao BZ, Olk DC, Jia ZJ, Mao JD, Cai YF, Zhang JB (2018) Contributions of residue-C and -N to plant growth and soil organic matter pools under planted and unplanted conditions. Soil Biol Biochem 120:91–104

Lian T, Wang G, Yu Z, Li YS, Liu XB, Jin J (2016) Carbon input from ^{13}C-labelled soybean residues in particulate organic carbon fractions in a Mollisol. Biol Fertil Soils 52:331–339

Lian T, Yu Z, Li Y, Jin J, Wang G, Liu XB, Tang CX, Franks A, Liu JJ, Liu JD (2019) The shift of bacterial community composition magnifies over time in response to different sources of soybean residues. Appl Soil Ecol 136:163–167

Lu J, Dijkstra FA, Wang P, Cheng WX (2019) Roots of non-woody perennials accelerated long-term soil organic matter decomposition through biological and physical mechanisms. Soil Biol Biochem 134:42–53

Marschner B, Kalbitz K (2003) Controls of bioavailability and biodegradability of dissolved organic matter in soils. Geoderma 113:211–235

Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. Embnet J 17:10–12

McCormack ML, Guo DL, Iversen CM, Chen WL, Eissenstat DM, Fernandez CW, Li L, Ma CG, Ma ZQ, Poorter H, Reich PB, Zadworny M, Zanne A (2017) Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. New Phytol 215:27–37

Murphy CJ, Baggs EM, Morley N, Wall DP, Paterson E (2015) Rhizosphere priming can promote mobilisation of N-rich compounds from soil organic matter. Soil Biol Biochem 81:236–243

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:678–681

Olsen SR, Cole CV, Watanabe FS, Dean LA (1954) Estimation of available phosphorous in soil by extraction with sodium bicarbonate. USDA circular 939. USAD, Washington DC, USA

Pittelkow CM, Liang X, Linquist BA, van Groenigen KJ, Lee J, Lundy ME, van Gestel N, Six J, Venterea RT, van Kessel C (2015) Productivity limits and potentials of the principles of conservation agriculture. Nature 517:365–368

Quast C, Pruesse E, Yilmaz P, Gerken J, Schweer T, Yarza P, Peplies J, Glockner FO (2012) The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res 41:590–596

R Development Core Team (2016) R Foundation for statistical computing, Vienna, Austria

Rayment GE, Lyons DJ (2011) Soil chemical methods-Australasia. CSIRO Publishing. pp135

Robinson D (2001) δ^{15}N as an integrator of the nitrogen cycle. Trends Ecol Evol 16:153–162

Sasse J, Martinoia E, Northen T (2018) Feed your friends: do plant exudates shape the root microbiome? Trends Plant Sci 23:25–41

Su Y, He ZC, Yang YH, Jia SQ, Yu M, Chen XJ, Shen AL (2020) Linking soil microbial community dynamics to straw-carbon distribution in soil organic carbon. Sci Rep 10:5526

Vargas TD, Concilio A, Woyann LG, Santos RHS, Cheng WX (2020) Rhizosphere priming effect on N mineralization in vegetable and grain crop systems. Plant Soil 452:281–293

Vance E, Brookes P, Jenkinson D (1987) An extraction method for measuring soil microbial biomass C. Soil Biol Biochem 19:703–707

Wang G, Zhou K, Jin J, Pan XW, Liu XB (2003) Effects of different N sources on N nutrient and microbial distribution across soybean rhizosphere. Soil Sci Plant Nutr 49:817–823

Wang Y, Li M, Pei JB, An TT, Saeed MF, Shan T, Xu YD, Wang JK (2019a) Dynamics of maize straw-derived nitrogen in soil aggregates as affected by fertilization. J Soil Sediment 19:2882–2890

Wang YH, Yu ZH, Li YS, Wang GH, Tang CX, Liu XB, Liu JJ, Xie ZH, Jin J (2019b) ^{13}C-DNA-SIP distinguishes the prokaryotic community that metabolizes soybean residues produced under different CO_2 concentrations. Front Microbiol 10:2184

Weber CF, King GM (2017) Volcanic soils as sources of novel CO-oxidizing *Paraburkholderia* and *Burkholderia: Paraburkholderia hiiakae* sp. nov., *Paraburkholderia metrosideri* sp. nov., *Paraburkholderia paradisi* sp. nov., *Paraburkholderia peleae* sp. nov. and *Burkholderia alpina* sp. nov. a member of the *Burkholderia cepacia* complex. Front Microbiol 8:207

Weisskopf L, Heller S, Eberl L (2011) *Burkholderia* species are major inhabitants of white lupin cluster roots. Appl Environ Microbiol 77:7715–7720

Wu J, Joergensen RG, Pommerening B, Chaussod R, Brookes PC (1990) Measurement of soil microbial biomass C by fumigation-extration-an automated procedure. Soil Biol Biochem 22:1167–1169

Xie Z, Li Y, Yu Z, Wang GH, Tang CX, Mathesius U, Liu XB, Liu JJ, Liu JD, Herbert SJ, Wu JJ, Jin J (2021) Incorporation of maize crop residue maintains soybean yield through the stimulation of nitrogen fixation rather than residue-derived nitrogen in Mollisols. Field Crops Res 272:108269

Xu Q, O'Sullivan JB, Wang XJ, Tang CX (2019) Elevated CO_2 alters the rhizosphere effect on crop residue decomposition. Plant Soil 436:413–426

Youssef RA, Chino M (1988) Development of a new rhizobox system to study the nutrient status in the rhizosphere. Soil Sci Plant Nutr 34:461–465

Yu DL, Wen ZG, Li XM, Song XJ, Wu HJ, Yang PL (2018) Effects of straw return on bacterial communities in a wheat-maize rotation system in the North China Plain. PLoS One 13:e0198087

Yu ZH, Wang Y, Yan N, Li YS, Xie ZH, Jin J (2017) Effects of elevated CO_2 on the abundance of rhizosphere bacteria, fungi and denitrification bacteria in different soybean cultivars. Soil Crops 6:9–16

Zhang DQ, Hui DF, Luo YQ, Zhou GY (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J Plant Ecol 1:85–93

Zhao JW, Duan LP, Qian LL, Cao P, Tian YY, Ju HX, Xiang WS, Wang XJ (2019) *Kribbella jiaozuonensis* sp. nov., a novel actinomycete isolated from soil. Int J Syst Evol Microbiol 69:3500–3507

Zheng FJ, Wu XP, Zhang MN, Liu XT, Song XJ, Lu JJ, Wang BS, van Groenigen KJ, Li SP (2022) Linking soil microbial community traits and organic carbon accumulation rate under long-term conservation tillage practices. Soil Till Res 220:105360

Zwetsloot MJ, Ucros JM, Wickings K, Wilhelm RC, Sparks J, Buckley DH, Bauerle TL (2020) Prevalent root-derived phenolics drive shifts in microbial community composition and prime decomposition in forest soil. Soil Biol Biochem 145:107797