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Impact of root diversity upon coupling between soil C and N accumulation and bacterial community dynamics and activity: Result of a 30 year rotation experiment

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ABSTRACT

Many ecosystem functions and processes depend on biodiversity, however, the effect of root diversity in agroecosystems on soil bacterial communities and processes remained largely unknown. Our objectives were to examine the importance of increased root diversity through crop rotation on soil bacterial community composition and its relationship with soil carbon (C) and nitrogen (N) accumulation, which play an important role in soil fertility. In a field experiment with 30-year crop rotation, where there was no difference in root biomass input in top soil, soil C and N accumulation rates, soil microbial activities and bacterial community composition were investigated. Soil C and N accumulation rates and microbial biomass content were generally increased after rotation, with a greater increase in legume-cereal rotation than in cereal-cereal rotation. Crop rotation also increased soil microbial activity (soil respiration, potential N mineralization), but did not affect soil bacterial diversity. The increased bacterial abundance and changes in bacterial community structure and abundances of dominant bacterial phyla in rotation soils were related to increases in soil C and N accumulation and microbial activity. Our results suggest that increased root diversity through rotation can influence soil bacterial community structure and increase soil fertility by enhancing C and N accumulation rates, and cause positive effects on soil organic C and fertility. The influence of legume-cereal rotation was greater than that of cereal-cereal rotation.

1. Introduction

High plant diversity improves plant productivity, increases resource use efficiency and soil nutrient availability, and potentially increases ecosystem stability, which has been tested primarily in prairie grasslands (Tilman et al., 2006; Fraser et al., 2015). Similarly, crop rotation in agriculture, which increases crop diversity compared to monoculture, can mitigate weed, insect and pathogen pressure, and enhances crop yields by inclusion of legumes (McDaniel et al., 2014b and references therein). Moreover, belowground benefits of rotation, such as increases in soil organic carbon (C) and microbial biomass, have been identified in many studies (Gattinger et al., 2012; McDaniel et al., 2014b). However, the underlying mechanisms are not well understood. Root inputs are regarded as more important for soil organic C accumulation than shoot inputs (Schmidt et al., 2011). Thus, increased root inputs by increasing crop biomass are considered to be an important factor for soil C accumulation in rotation, especially in rotations including one or more cover crops (McDaniel et al., 2014b). Furthermore, several studies have shown that chemical diversity and complexity of C inputs to soil strongly influence long-term soil organic C dynamics (Johnson et al., 2007; Fornara and Tilman, 2008). Additionally, increased crop diversity in rotation has been found enhancing residue C transformation (McDaniel et al., 2014a). However, the effect of root diversity or complexity in rotation system on soil C accumulation is remained largely unknown. Moreover, whether the effects of increased root diversity by crop rotation on soil microbial communities and soil properties follow similar trends with changes in crop types are unclear.

Soil bacteria play an important role in ecosystem C and nitrogen (N) budgets through their multiple roles in soil C and N dynamics (Acosta-Martinez et al., 2008). Soil microbial activity such as soil enzyme activity, respiration rate and N mineralization rate and other indexes (Zak et al., 2003; Yao et al., 2014; Trivedi et al., 2016), has been shown to increase in legume rotations (Tiemann et al., 2015; Trivedi et al., 2015). Additionally, structure and composition of soil bacterial community has been shown to change in response to crop rotation regimes (Alvey et al., 2003; Wang et al., 2012; Tiemann et al., 2015; Trivedi et al., 2015). It has been suggested that microbial communities and activities in rotation are mainly affected by crop rotation diversity through its effect on quantity, quality and chemical diversity of residues (Tiemann et al., 2015; Trivedi et al., 2015). A shift in soil microbial community composition can lead to changes in C and N dynamics, as reported by

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Mooshammer et al. (2014), who suggested that microbial communities can regulate N-use efficiency (NUE) and C-use efficiency (CUE) to cope with resource imbalances. High CUE and NUE would result in increased C and N accumulation in soil (Manzoni et al., 2012; Mooshammer et al., 2014). However, it remains unclear how changes in microbial communities and activity influence soil C and N dynamics in response to increased root diversity through crop rotation.

The objectives of this study were to: (i) examine the effect of increased root diversity through rotation on soil bacterial community structure and composition; and (ii) determine the link between bacterial taxa, community structure and microbial activity and soil C and N accumulation. In this study we used Illumina MiSeq sequencing to determine bacterial community structure and composition in soil from a 30-year field experiment with legume based rotation, non-legume rotation and monoculture in the Loess Plateau in northwest China. The shifts of soil microbial communities associated with rotation in this long-term experiment have not been reported. Soil microbial activity was determined by soil respiration rate, N mineralization and microbial nutritional stoichiometry, and their links to soil C and N accumulation were also assessed. We hypothesized that (i) increased root diversity in rotation would increase soil bacterial diversity and abundance, and change bacterial community structure, (ii) shifts of bacterial taxa, community structure and changes in microbial activity would be related to soil C and N accumulation rates, and (iii) the presence of legume in rotation would have a greater impact than cereal-cereal rotation. Results in this study will provide insights into how root diversity in crop rotation affects soil microbial communities and increases microbial activity, and influences in soil organic C and fertility.

2. Materials and methods

2.1. Experimental site and sampling

The experiments were conducted in the Changwu Agro-ecological Experimental Station on the Loess Plateau 107°40′E, 35°12′N, altitude 1220 m, Shaanxi province, China. This site has a semi-arid climate with an annual rainfall of 584 mm (1957–2001) and annual average temperature of 9.1 °C, and represents a typical rain-fed agricultural area in the warm temperate zone of China. The soil is loam developed from loess deposits. The concentrations of soil total organic C and total N in 1984 were 6.5 $g \cdot kg^{-1}$ and 0.8 $g \cdot kg^{-1}$, respectively.

Four cropping treatments with three replicates were selected in the long-term experiment established in 1984. These treatments included: continuous winter wheat (*Triticum aestivum* L.) where winter wheat was grown every year with summer fallow (W); winter wheat-broomcorn millet (*Panicum miliaceum*, a local cultivar)-maize(*Zea mays* L., cv. 'Danyu 13') where winter wheat was grown one year with summer fallow and one year with broomcorn millet followed by one-year maize (WBM); winter wheat-sainfoin (*Onobrychis viciaefolia*, a local cultivar) where winter wheat was grown two years followed by one-year sainfoin (WS); winter wheat-potato (*Solanum tuberosum* L.)-alfalfa where winter wheat was grown two years followed by four years' alfalfa grown (WPA) and one-year potato (Fig. 1). The fertilizers N and P applied in the form of urea (120 $kg \cdot N \cdot ha^{-1}$ per year) and superphosphate (40 $kg \cdot P_2O_5 \cdot ha^{-1}$ per year). The aboveground biomass of sainfoin and alfalfa was removed two times (late June and mid August) per year by mowing, while the aboveground biomass of wheat, broomcorn millet and potato, and potato tuber were removed at harvest.

Crops are not irrigated, thus, winter wheat-summer fallow is a common practice in this area to maintain soil water and crop yield. Crop yield fluctuates with precipitation (Hao et al., 2004), indicating that water is the most limiting factor for crop production. More intense cropping in rotation induces over-use of soil water by one crop and decreasing biomass production of the following crop in most years. The aboveground biomass of sainfoin and alfalfa were removed two times per year (late June and mid August) by mowing, while the aboveground biomass of wheat, broomcorn millet and potato, and potato tuber were removed at harvest. Similarly, root inputs into the top soil did not differ among rotations.

Soil samples in the four cropping treatments were collected at May 2014 (filling stage of winter wheat) at depth 0–20 cm, to explore the root diversity effect on soil bacterial community and its relationship to soil C and N accumulation. To reduce the current crop effect in the rotation system, we collected soils when all treatments were under winter wheat (Fig. 1). Five cores were taken from each plot in the middle between wheat rows and mixed to reduce within-plot variability. All samples were passed through a 2.0–mm sieve, stored at −80 °C for DNA extraction and at 4 °C for other analyses.

2.2. Soil properties

Soil moisture was determined by oven-drying the samples at 105 °C for 48 h. Soil pH was determined with a soil to water ratio of 1:5. Total organic carbon (TOC) was determined with dichromate oxidation method (Nelson et al., 1982), total nitrogen (TN) with the Kjeldahl method (Bremner and Mulvaney, 1982). Soil microbial biomass C and N (MBC and MBN) were measured by the chloroform fumigation-extraction method (Joergensen and Brookes, 1990) except 4 g soil and 16 ml 0.5 $M \cdot K_2SO_4$ extractant were used. The organic C in the extract

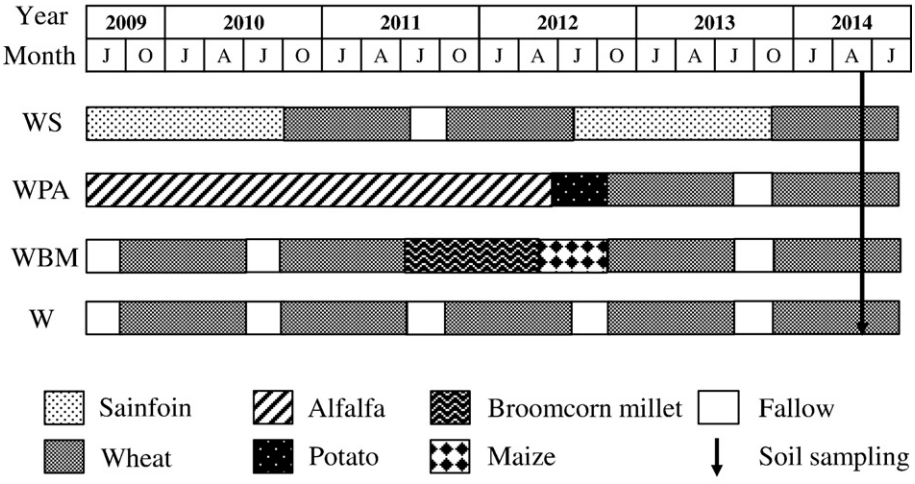

Fig. 1. The rotation schemes in rotation and monoculture systems (WS, WPA, WBM and W). WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

was determined using an automated total organic C (TOC) analyzer (Shimadzu, TOC-Vwp, Japan), and the N was measured by the Kjeldahl method. No conversion factor was used because it had not been determined in the soil used in this study.

There was no difference in soil bulk density between beginning (1984) and end (2014) of the study period. Thus, the average bulk density (1.30 $Mg \cdot m^{-3}$) was used to convert soil total organic C concentration to soil organic C mass per unit area. Annual accumulation rate of organic C in soil ($Mg \cdot ha^{-1}\ yr^{-1}$) was calculated as follows:

$$\text{Accumulation rate} = (\text{element storage in 2014} - \text{element storage in 1984})/30 \quad (1)$$

where element storage was calculated using the equation:

$$\text{Element storage} = \text{element concentration} \times \text{soil bulk density} \times 20\ (\text{soil layer thickness, cm}) \times 10^{-1} \quad (2)$$

2.3. Soil microbial activity

Potential N mineralization rate (Miner–N) was measured according to the laboratory incubation method described by Fornara et al. (2009). Soil basal respiration (R) was measured according to the method described by Enwall et al. (2007). The respiratory quotient Qco_2 was calculated by the ratio of soil respiration per day to microbial biomass C (Anderson and Domsch, 1986). The microbial community C-use efficiency/N-use efficiency (CUE/NUE) ratio was calculated according to the formula in Mooshammer et al. (2014) and Zhong et al. (2015):

$$CUE : NUE = B_{C:N} : R_{C:N} \quad (3)$$

where $B_{C:N}$ is the C:N ratio of the microbial biomass and $R_{C:N}$ is the C:N ratio of the soil.

2.4. Soil DNA extraction and MiSeq sequencing of 16S rRNA gene amplicons

Soil DNA was extracted from 0.5 g soil using the FastDNA® Spin Kit for Soil (MP Biomedicals, Cleveland, OH, USA) and the FastPrep-24 instrument according to the manufacturer's instructions. The purified DNA was diluted with 50 μl sterilized water and checked for quality and quantity using a NanoDrop Spectrophotometer.

DNA was amplified using the primers 515F (5′-GTGCCAGCM GCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) designed to be universal for bacteria and archaea (Caporaso et al., 2011). Primers were tagged with unique barcodes for each replicate DNA sample. PCR reactions were carried out in a 30 μl mixture with 15 μl of Phusion® High-Fidelity PCR Master Mix (New England Biolabs), 0.2 μM of each primer and about 10 ng template DNA. The thermal cycling was as follows: 98 °C for 1 min; 30 cycles of 98 °C for 10 s, 50 °C for 30 s, and 72 °C for 1 min; 72 °C for 5 min. Negative controls using sterilized water instead of soil DNA were included to check for primer or sample DNA contamination. Each DNA sample was amplified in three technical replicates and then verified with electrophoresis and mixed in one tube. All samples were pooled together with equal molar amounts from each sample and purified with the GeneJET gel extraction kit (Thermo Scientific). The purified library was generated using NEB Next® Ultra™ DNA Library Kit for Illumina (NEB, USA) and mixed with the index codes. The library quality was assessed in the Quibt® 2.0 Fluorometer (Thermo Scientific) and Agilent Bioanalyzer 2100 system. Then, the library was sequenced on an Illumina MiSeq platform by which 250 bp/300 bp paired-end reads were generated.

All sequence reads were merged using FLASH (Magoc and Salzberg, 2011) and assigned to each sample according to their barcodes. Sequence analysis was performed by UPARSE software package using the UPARSE-OTU and UPARSE-OTUref algorithms (Edgar, 2013). The processed sequences were used for a chimera check using the Uchime algorithm (Edgar et al., 2011). Sequences with ≥97% similarity were clustered into operational taxonomic units (OTUs). Taxonomy was assigned using the Ribosomal Database Project classifier (Wang et al., 2007). Each sample was rarefied to the same number of reads (29,507 sequences) for both alpha-diversity (chao1 estimator of richness, observed species and Shannon's diversity index) and beta-diversity (NMDS, PCA) analyses. The original sequence data are available at the European Nucleotide Archive (ENA) with accession number PRJEB16323 (http://www.ebi.ac.uk/ena/data/view/PRJEB16323).

2.5. Statistical analysis

This study was analyzed as a completely randomized design with four treatments and three replicate plots per treatment in which each plot was a repeatedly measured unit. Differences in relative abundances of microbial taxa and soil properties between samples were tested by one-way-analysis of variance (ANOVA); post-hoc analyses (where appropriate) were performed using Tukey's multiple comparison test at $P < 0.05$ (GenStat® for Windows 12.0; VSN Int. Ltd., UK). Correlations between species abundance, microbial activities and soil properties were analyzed using Spearman's method by SPSS 17.0 software.

With the untransformed microbial relative abundance at the OTU level as input data, the community structure was evaluated by non-metric multidimensional scaling (NMDS) with *PC-ORD* 5.0 (MjM software, www.pcord.com). The 2D stress indicates how well the plot represents the variability in the data. A 2D stress <10 is considered to represent a good reflection of the resemblance matrix (Peck, 2010). Significant differences in community structure between treatments were determined by multi-response permutation procedures (MRPP) (*PC-ORD* 5.0, MjM software, www.pcord.com). Principal component analysis (PCA) and redundancy analysis (RDA) analysis were carried out with Canoco 4.5 (Ter Braak and Smilauer, 2002). Monte Carlo permutation (999 repetitions) was used to test the relationships between the soil properties, microbial activities and microbial groups.

3. Results

3.1. Soil chemical properties and microbial biomass

All measured soil chemical and microbial properties were affected by cropping regimes. Concentrations of total organic C, total N and microbial biomass C (MBC) were generally higher in WS and WPA soils than that in W and WBM soils (Table 1). Soil microbial biomass N (MBN) concentration was higher in WS soil than in monoculture (W) and other rotation soils. Compared to W, soil C accumulation rate was increased by 106, 61 and 29% in WS, WPA and WBM soils, respectively (Fig. 2A). The N accumulation rate was higher in legume based rotation soils (WS and WPA) than in cereal-cereal rotation (WBM) and monoculture soils (Fig. 2B). The PCA ordination revealed a clear difference between cropping systems (Fig. S1). The first two axes explained about 91% of the variance, with PCA1 and PCA2 explaining 73.8% and 17.2% of variation, respectively.

3.2. Soil microbial activity

Soil respiration rate and CUE/NUE were generally higher in rotation soils (WS, WPA and WBM) than in W soil (Fig. 3). However, Qco_2 was 27% higher in W soil than in WBM soil and138–175% higher than in WPA and WS soils. Soil potential N mineralization rate was 60–87% higher in WS and WPA soils than in WBM soil and 150–190% higher than in W soil.

Table 1
Soil chemical and microbial properties.

Soil properties[†]	WS	WPA	WBM	W
pH	8.54 ± 0.04 a	8.54 ± 0.05 a	8.46 ± 0.04 a	8.44 ± 0.13 a
TOC (g kg^{-1})	9.62 ± 0.38 a	9.05 ± 0.22 ab	8.3 ± 0.4 ab	7.9 ± 0.3 b
TN (g kg^{-1})	1.16 ± 0.05 a	1.13 ± 0.01 ab	0.99 ± 0.05 ab	0.95 ± 0.04 b
MBC (mg kg^{-1})	180.72 ± 12.32 a	168.48 ± 6.28 a	82.52 ± 2.88 b	51.56 ± 4.31 b
MBN (mg kg^{-1})	26.41 ± 0.57 a	15.07 ± 0.21 b	15.98 ± 0.47 b	17.34 ± 0.1 b
Bacteria (copies g^{-1}, $\times 10^8$)	52.25 ± 2.06 a	50.02 ± 0.71 a	46 ± 1.77 ab	41.6 ± 0.4 b
Crop biomass (t ha^{-1} yr^{-1}) [‡]	8.5	7.7	7.1	7.5
Root C input (t ha^{-1} yr^{-1}) [‡]	1.3	1.1	1.1	1.2

[†] TOC: total organic C; TN: total N; MBC: microbial biomass C; MBN: microbial biomass N. Values with different letters in a row mean significant difference at $P < 0.05$. Values are means of three replicates ± standard error. WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

[‡] The average aboveground biomass production and root C input to soil in 0-20 cm from 1984 to 2007 derived from Guo et al. (2008). No significant difference was found for crop biomass and root C input in top soil between treatments.

3.3. Soil bacterial abundance

The abundance of bacteria quantified by real-time PCR was highest in WS soil and lowest in W soil (Table 1). Soil bacterial abundance was significantly and positively correlated with soil C and N accumulation rates (Table 2), soil total organic C, total N, microbial biomass C and microbial activity except Qco_2 (Table S1).

3.4. Soil prokaryotic diversity and structure

In total, 891,086 high quality and chimera-free reads were obtained by MiSeq sequencing of 16S rRNA gene amplicons with 29,507 to 98,599 reads per sample. Good's coverage values were higher than 0.97 with a 97% similarity cutoff for all soils, which indicated that the current numbers of sequence reads were sufficient to determine the bacterial diversity in these soils. The number of observed species was highest in W soil and lowest in WPA soil, while Chao1 richness and Shannon index were not affected by rotation (Table S2).

The proportion of OTUs shared between W and rotation soils was 75.5–81.3% in W soil, 83.9% in WS soil, 84.0% in WPA soil and 76.5% in WBM soil (data not shown). This was further supported by the changes of prokaryotic community structure in W and rotation soils. The overall prokaryotic community structure differed between W and rotation soils and also differed among rotation soils (Fig. S2).

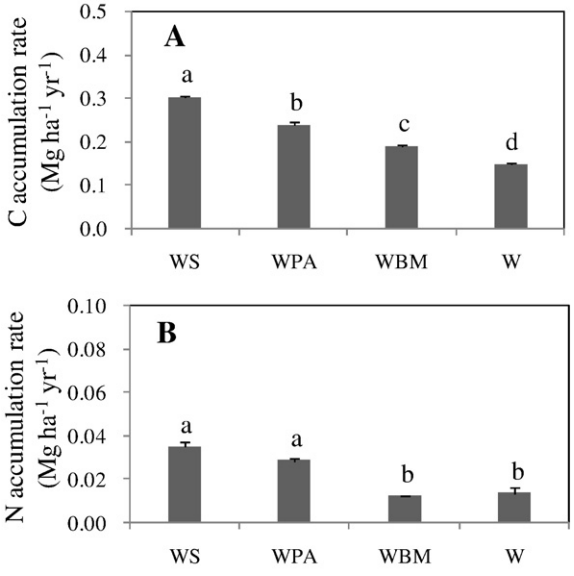

Fig. 2. Soil organic C and total N accumulation rates following 30-year crop rotation and monoculture trials. Error bars are standard errors ($n = 3$). Different letters indicate significant difference at $P < 0.05$ among W and rotation soils. WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

3.5. Relative abundances of prokaryotic taxa

The bacterial phyla with relative abundances higher than 1% generally differed between W and rotation soils (Fig. 4). *Proteobacteria*, *Actinobacteria* and *Acidobacteria* were predominant phyla in W and rotation soils, with relative abundances of 11–29% (Fig. 4). The relative abundances of *Proteobacteria* and *Bacteroidetes* were higher in WS and WPA soils than in WBM and W soils. *Actinobacteria* relative abundance was highest in WPA soil and lowest in WBM soil, whereas the reverse was true for Armatimonadetes which was lowest in WPA soil and highest in WBM soil. The relative abundances of *Acidobacteria*, *Verrucomicrobia* and *Crenarchaeota* were generally higher in W soil than that in rotation soils, while *Gemmatimonadetes* and *Nitrospirae* increased in abundance in WPA and WBM soils. The relative abundance of *Planctomycetes* was higher in W and WBM soils than in WS and WPA soils, while *Firmicutes* had highest abundance in WBM soil.

There were no significant differences ($P > 0.05$) between cropping systems for *Deltaproteobacteria*, Phycisphaerae and Thermomicrobia, but there were significant differences ($P < 0.05$) between cropping systems for twelve of the most abundant classes (Fig. 5). The relative abundances of proteobacterial classes showed different responses to cropping systems. *Betaproteobacteria* and Gammaproteobacteria abundance was high in all rotation soils, while abundance of Alphaproteobacteria was low in WBM soil (Fig. 5A–C). For the phylum *Acidobacteria*, classes Chloracidobacteria and *Acidobacteria* subdivision 6 had lower abundance in rotation soils compared to W soil, with greater decreases in WPA and WBM soils than in WS soil (Fig. 5D and E). The relative abundance of *Actinobacteria*, Thermoleophilia and Sphingobacteriia was low in WBM soil, whereas Acidimicrobia and *Gemmatimonadetes* generally had high abundance in rotation soils (Fig. 5F–J). The class *Thaumarchaeota* had lower abundance in rotation soils compared to W soil, with a greater decrease in WBM soil than in WS and WPA soils (Fig. 5K). Nitrospira abundance was highest in WBM soil and lowest in WS soil (Fig. 5L).

3.6. Correlations between soil properties, microbial activity and bacterial communities

Soil C and N accumulation rates were significantly and positively correlated with bacterial abundance, microbial biomass C and microbial activities including soil respiration rate, N mineralization and CUE/NUE, and negatively correlated with Qco_2 (Table 2). Additionally, soil C and N accumulation rates, respiration rate, potential N mineralization rate and CUE/NUE were positively correlated with *Actinobacteria*, *Bacteroidetes* and copiotrophs in *Proteobacteria*, and negatively correlated with *Acidobacteria* and *Planctomycetes* (Table 3). Monte Carlo permutation test showed that the bacterial community structure was significantly

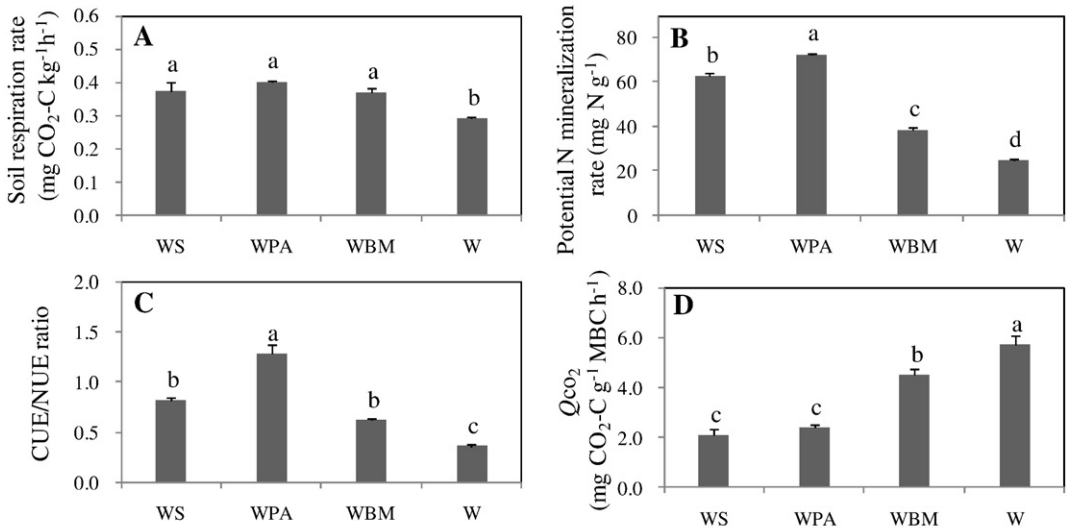

Fig. 3. Soil respiration rate (A), potential N mineralization rate (B), CUE/NUE ratio (C) and Qco_2 (D) under different treatments in 30-year crop rotation trial. Error bars are standard errors ($n = 3$). Different letters indicate significant difference at $P < 0.05$ among W and rotation soils. CUE/NUE ratio: C-use efficiency/N-use efficiency ratio; Qco_2: respiratory quotient. WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

correlated with soil C ($F = 7.73$, $P = 0.008$) and N accumulation rates ($F = 5.24$, $P = 0.02$) and CUE/NUE ($F = 5.76$, $P = 0.01$) (Fig. 6).

4. Discussion

This study showed that increased root diversity in 30-year crop rotation trial had a great impact on soil bacterial community composition, and increased soil bacterial abundance and C and N accumulation. These changes were greater in legume-cereal rotations than in cereal-cereal rotation. Although our results represent a single time point, previous studies have shown that long term patterns within soil microbial communities generally remain intact and reflect differences in management practices rather than seasons and plant types (Lupatini et al., 2013; Williams et al., 2013).

4.1. Cropping regimes changed soil microbial activity

Soil microbial activity indicated by potential soil respiration has been found decreased (Meriles et al., 2009) or increased in crop rotation soil (Tiemann et al., 2015; Trivedi et al., 2015). In this study, we found that soil microbial activities, including soil respiration, potential N mineralization and CUE/NUE were generally higher in rotation soils than in wheat monoculture soil (Fig. 3). This suggests that increasing crop diversity will be beneficial for fragile ecosystems such as Loess Plateau with low soil fertility. The Qco_2 decreased in the following order W > WBM > WS and WPA. A low Qco_2 means that most of the substrate C is used for growth and only a small proportion is respired (Meyer et al., 1996). Thus,

Table 2
Spearman correlations of soil microbial abundance, biomass and activities with soil C and N accumulation rates.

	C accumulation rate	N accumulation rate
Bacterial abundance	0.85**	0.66*
MBC	0.82**	0.79**
MBN	0.20	0.33
R	0.59*	0.62*
Miner-N	0.77**	0.67*
CUE/NUE	0.69*	0.66*
Qco_2	−0.87**	−0.84**

Bacterial abundance: the number of bacterial 16S rRNA gene copies; MBC: microbial biomass C; MBN: microbial biomass N; TOC: total organic C; TN: total N; R: respiration rate; Miner-N: potential N mineralization rate; CUE/NUE: C-use efficiency/N-use efficiency ratio; Qco_2: respiratory quotient.
** $P < 0.01$.
* $P < 0.05$.

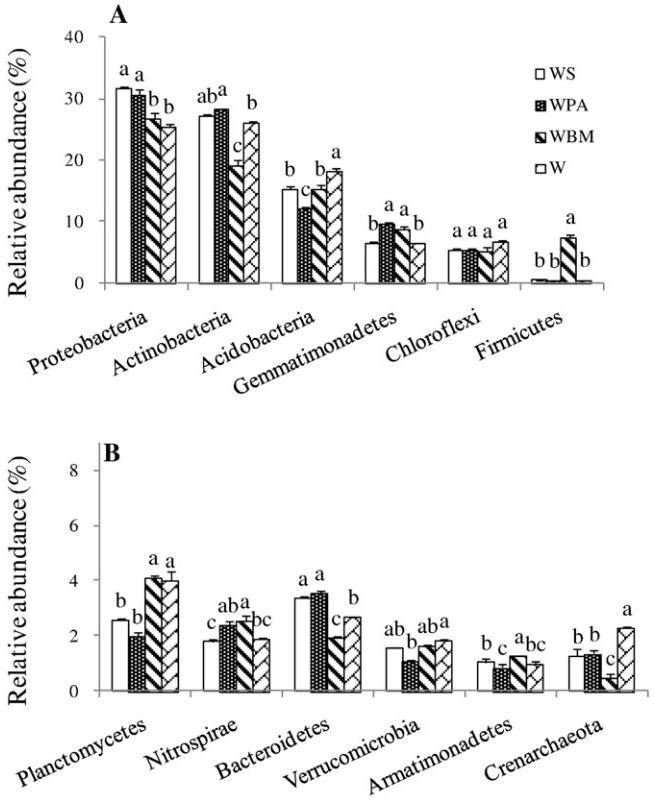

Fig. 4. Relative abundances of soil dominant phyla under different treatments in 30-year crop rotation trial. The relative abundance is represented as a proportion of 16S rRNA gene reads at the phylum level of the total number of reads. Error bars are standard errors ($n = 3$). Different letters indicate significant difference at $P < 0.05$ among W and rotation soils. WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

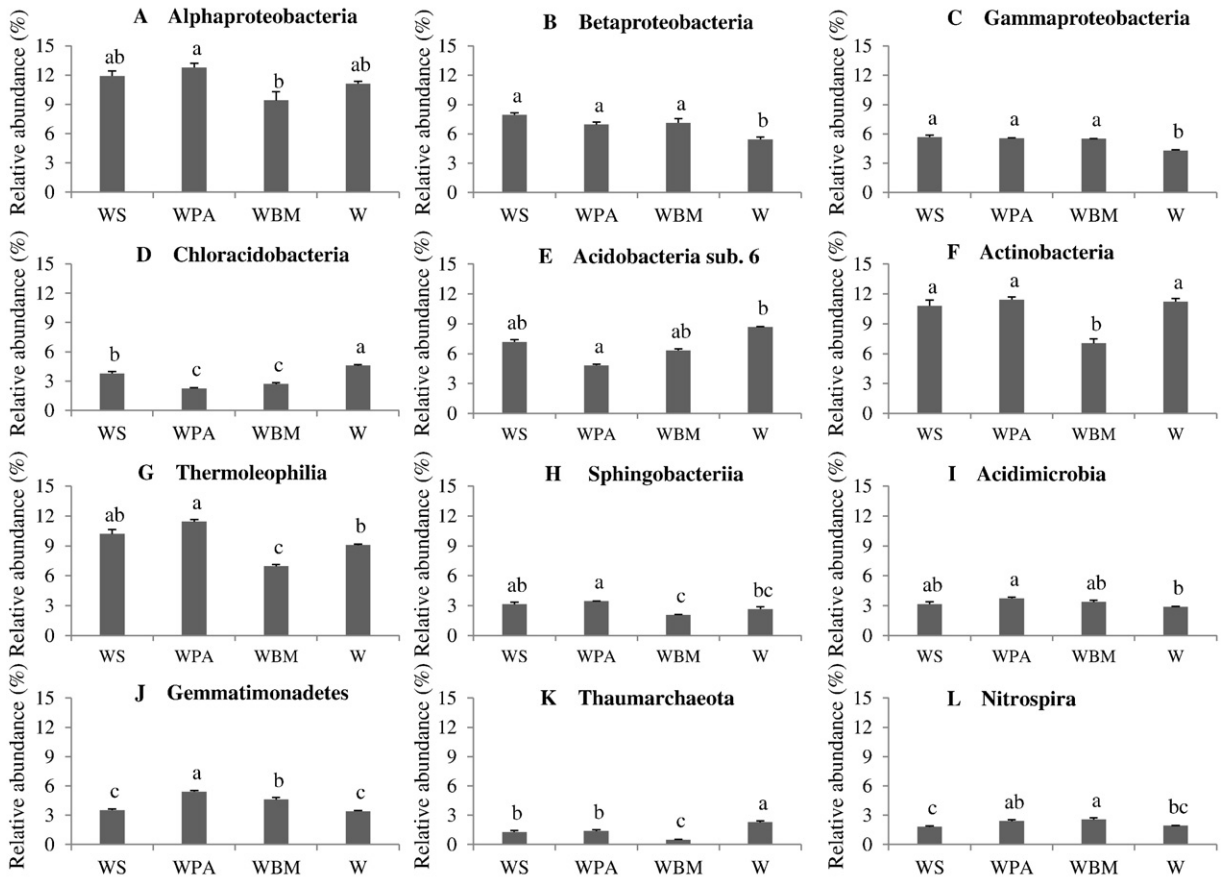

Fig. 5. Relative abundances of twelve most abundant classes under different treatments in 30-year crop rotation trial. The relative abundance is represented as a proportion of 16S rRNA gene reads at the class level of the total number of reads. Error bars are standard errors ($n = 3$). Different letters indicate significant difference at $P < 0.05$ among W and rotation soils. *Acidobacteria* sub. 6: *Acidobacteria* subdivision 6. WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

microbial CUE is high which may promote C stabilization in soils (Manzoni et al., 2012). In agreement with this, microbial biomass C concentration and C accumulation rate were higher in rotation soils than in monoculture soil.

Legume-wheat rotation soils had higher CUE/NUE, microbial biomass C and C accumulation rate and lower Qco_2 than cereal-cereal rotation soil, suggesting that legumes promote higher CUE and C deposition than cereals. This was confirmed by the higher total organic C concentration in legume-cereal rotation soils than in cereal-cereal rotation soil, and consistent with other studies that show higher soil organic C in legume based cropping systems (Gattinger et al., 2012; Feiziene et al., 2015).

4.2. Crop rotation increased bacterial abundance but did not affect bacterial diversity

Soil bacterial abundance quantified by real-time PCR was higher in rotation than in monoculture soil, with a greater increase in legume-cereal rotation than in cereal-cereal rotation (Table 1). In contrast, Trivedi et al. (2015) reported that bacterial abundance was unaffected or

Table 3
Spearman correlations of microbial biomass, activities and soil C and N accumulation rates with predominant bacterial phyla.

	MBC[a]	MBN[a]	R[a]	Miner-N[a]	CUE/NUE[a]	Qco_2[a]	C accumulation rate[a]	N accumulation rate[a]
Proteobacteria	0.75**	0.07	0.72**	0.75**	0.74**	−0.75**	0.85**	0.82**
Copiotrophs[b]	0.88**	−0.01	0.74**	0.85**	0.81**	−0.085**	0.80**	0.79**
Oligotrophs[b]	0.50	−0.39	0.76**	0.57	0.64*	−0.32	0.32	0.24
Actinobacteria	0.69*	−0.15	0.48	0.73**	0.71**	−0.64*	0.59*	0.73**
Acidobacteria	−0.74**	0.49	−0.73**	−0.81**	−0.92**	0.62*	−0.60*	−0.51
Gemmatimonadetes	0.32	−0.79**	0.58*	0.53	0.60*	−0.12	0.07	−0.08
Planctomycetes	−0.65*	0.26	−0.64*	−0.83**	−0.71**	0.58*	−0.66*	−0.66*
Bacteroidetes	0.71*	−0.06	0.48	0.71*	0.72*	−0.66*	0.60*	0.75**

** $P < 0.01$.
* $P < 0.05$.
[a] MBC: microbial biomass C; MBN: microbial biomass N; R: respiration rate; Miner-N: potential N mineralization rate; CUE/NUE: C-use efficiency/N-use efficiency ratio; Qco_2: respiratory quotient.
[b] Copiotrophs: including α, β and γ-*Proteobacteria*; Oligotrophs: δ-*Proteobacteria*.

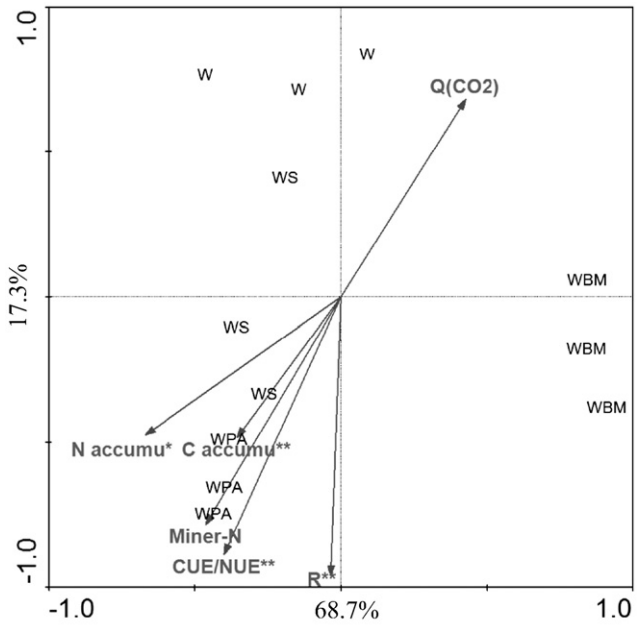

Fig. 6. Redundancy analysis (RDA) of soil bacterial communities and soil microbial activities and C and N accumulation rates. Miner-N: N mineralization; R: soil respiration; CUE/NUE: carbon-use efficiency/nitrogen-use efficiency; Qco_2: respiratory quotient; C accumu: C accumulation rate; N accumu: N accumulation rate. **indicates that the correlations are significant at $P < 0.01$, *indicates that the correlations are significant at $P < 0.05$. WS: winter wheat-sainfoin rotation; WPA: winter wheat-potato-alfalfa rotation; WBM: winter wheat-broomcorn millet-maize rotation; W: winter wheat monoculture.

reduced in rotation soil compared to monoculture soil. Changes in bacterial abundance are coupled with changed resource availabilities (Fierer et al., 2007). Therefore it is possible that resource availability changed to a greater extent in this study than in that by Trivedi et al. (2015). However, bacterial diversity was not significantly affected by cropping regime, which is consistent with previous finding (Trivedi et al., 2015). This indicates that soil bacterial diversity was stable after 30-year of crop rotations.

4.3. Crop rotation changed soil bacterial community composition

The relative abundance of *Proteobacteria*, *Actinobacteria* and *Bacteroidetes* was generally higher in legume-wheat rotation soils than in non-legume soils. On the other hand, *Acidobacteria* and *Planctomycetes* abundance was generally higher in non-legume soils (Fig. 4). Based on the copiotrophic hypothesis, α, β and γ-*Proteobacteria* and *Bacteroidetes* have been classified as copiotrophs preferring to utilize relatively labile forms of C and high nutrient environments (Fierer et al., 2007; Ramirez-Villanueva et al., 2015). In contrast, δ-*Proteobacteria*, *Acidobacteria* and *Planctomycetes* are classified as oligotrophs thriving in low-nutrient conditions (Ramirez et al., 2010) and using relatively recalcitrant C forms (Ramirez-Villanueva et al., 2015). This was confirmed by the positive correlations between soil microbial biomass C, total organic C and total N and the relative abundances of *Bacteroidetes* and copiotrophs in *Proteobacteria*, and negative correlations with the relative abundances of *Acidobacteria* and *Planctomycetes* (Table 3). However, the relative abundance of δ-*Proteobacteria* was not affected by cropping regime. This might be explained by the low soil N content in all treatments. Zhou et al. (2015) found that high abundance of δ-*Proteobacteria* was coupled with low N content. *Actinobacteria* has been reported to have different life styles according to its habitat nutrient conditions (Trivedi et al., 2013; Trivedi et al., 2015; Wang et al., 2015), and their abundance has been reported to increase (Xuan et al., 2011) or decrease in legume-based rotation soils (Trivedi et al., 2015). In the present study, *Actinobacteria* abundance was higher in legume-based rotation soils suggesting that they are copiotrophs. In agreement with this we found in a previous study in the same long-term experiment that *Actinobacteria* abundance was higher in treatments receiving N fertilizer (Wang et al., 2015).

Gemmatimonadetes increased in abundance in WPA and WBM soils (Fig. 3) which might be due to lower soil moisture (Li and Huang, 2008) because *Gemmatimonadetes* are adapted to low soil moisture (DeBruyn et al., 2011). Many members of *Firmicutes* have the ability to produce spores (Galperin, 2013) to overcome periods of nutrient scarcity and extreme environmental conditions. The increased abundance of *Firmicutes* in WBM soil might be explained by the long cropping time which induced low nutrient and water availability throughout the year. *Verrucomicrobia* abundance was high in W soil which is in agreement with Trivedi et al. (2015) who reported higher abundance of *Verrucomicrobia* in wheat continuous soil compared to rotation soil (Trivedi et al., 2015). *Verrucomicrobia* is an important group of soil bacterial communities (Bergmann et al., 2011), however, its ecology in soil is poorly understood.

Nitrogen cycling communities were significantly affected by cropping regimes but showed different responses. Although abundance of *Nitrospirae* was generally low (1.8–2.5%), it was higher in WPA and WBM soils than the other treatments (Fig. 4). *Nitrospirae* have been shown variable responses to management practices with decreased abundance (Yao et al., 2014), increased abundance (Lopes et al., 2014) or no response (Wang et al., 2015). Abundance of *Crenarchaeota* dominated by genus *Candidatus* Nitrososphaera, which is an ammonia-oxidizing archaea, was low in rotation soils with higher total organic C and total N contents. This was similar as our previous study (Wang et al., 2015), which showed that the relative abundance of *Crenarchaeota* was lower in treatments receiving fertilizer than in unfertilized soil.

Compared to wheat monoculture, the relative abundance of *Betaproteobacteria* and Gammaproteobacteria was high in both legume-cereal and cereal-cereal rotation soils, whereas that of *Acidobacteria* subdivision 6, Chloracidobacteria and *Thaumarchaeota* was low. This indicates that cereal-cereal rotation influences soil bacterial communities on a lower taxonomic level than legume-cereal rotations.

Although all soils sampled in this study were under the same crop (winter wheat), crop rotation history strongly influenced soil bacterial community structure and composition. Abundance of copiotrophic groups was high at phylum level for legume-cereal rotation and at class level for cereal-cereal rotation, suggesting that soil bacterial community shifted from an oligotrophic to a copiotrophic regime. This may have multiple feedbacks in ecosystem processes, particularly in relation to C cycling. Increasing crop type diversity through rotation may lead to increased microbial growth and activity, which was confirmed by the increased microbial CUE in this study and enhanced retention of N in microbial biomass in McDaniel et al. (2014a). This might result in higher soil total organic C and total N in long-term rotation systems which are found in many studies.

4.4. Relationships among microbial activities, bacterial communities and soil C and N accumulation

Soil C and N accumulation rates were correlated to soil microbial activities and microbial biomass C concentration (Table 2), suggesting that cropping regime effects on soil C and N accumulation rates are likely mediated by the changes in microbial activities and biomass. Changes in microbial activities and biomass might be due to altered soil bacterial community structure. Soil bacterial community structure was significantly correlated with soil C and N accumulation rates and microbial CUE/NUE in rotation soils revealed by RDA ordination analysis (Fig. 6). These results suggest that soil bacteria in rotation shifted to a community potentially having higher C use efficiency, which cause higher C accumulation rate in soil. High microbial CUE/NUE and low Qco_2 in rotation soils were related to dominant bacterial phyla such as *Actinobacteria*,

Bacteroidetes and copiotrophs in *Proteobacteria* (Table 3). Kallenbach et al. (2015) reported that high microbial growth rates and high CUE were related to high C retention in soil by using ^{13}C substrate. This was confirmed in the present study in which high CUE/NUE and low Qco_2 in rotation soils were correlated with high abundance of copiotrophs, and resulted in a higher C accumulation rate in rotation soils. However, copiotrophic microbial groups are typically characterized by higher growth rates but lower CUE relative to slow-growing oligotrophs (Fierer et al., 2007). This is true in some studies in N application soils in which high soil respiration led to low CUE (Zhong et al., 2015), but not in this study in which both CUE and respiration were higher in rotations. This might be explained by McDaniel et al. (2014a) who reported that the residue diversity was increased in rotation soils which may facilitate more efficient and rapid microbial growth. Further work is needed to determine the direct or causal relationship between soil bacterial communities and CUE for example with stable isotope probing.

High microbial NUE indicates a reduced potential for soil N losses due to reduced substrates for nitrification and denitrification (Mooshammer et al., 2014), which might cause less nitrate leaching and gaseous N losses. In this study, rotation soils generally had higher N accumulation rates and microbial N concentrations compared to monoculture soil, indicating that microbial NUE increases in rotation soils. This is consistent with a lower abundance of nitrifying communities in rotations.

Previous studies focused on cropping regime effects mainly analyzed the changes of soil biochemical properties and soil microbial community structure by PLFA, DGGE, or T-RFLP (Alvey et al., 2003; Wang et al., 2012; Tiemann et al., 2015). Some studies also used high-throughput sequencing technologies (Yin et al., 2010; Xuan et al., 2011), however, few of these examined the effect of root diversity in rotation on soil bacterial community composition and its relationship with soil C and N accumulation. Tiemann et al. (2015) reported that as crop diversity increased from one to five species in rotation, distinct soil microbial communities were related to increases in soil organic C, total N and microbial activity. However, the biomass input was also significantly increased in that rotation study, thus, the crop diversity effect on soil microbial community composition and C input rates could not be separated from the root diversity effect through rotation. Moreover, abundance of *Actinobacteria* and *Bacteroidetes* increased in non-legume soils in some studies (Trivedi et al., 2015). This is in contrast to the results in this study in rain-fed semiarid soil. *Planctomycetes* was one of dominant phyla and did not show consistent response to nutrient application or cropping regimes (Yao et al., 2014; Zhong et al., 2015). But in the present study the relative abundance of *Planctomycetes* was 56–107% lower in legume-cereal rotation than in monoculture soil. This is unlikely to be due to soil water content because soil water content was not a dominant factor contributing to soil respiration on top soil in our previous study (Jiang et al., 2015). Consequently, our study suggests that increased root diversity through rotation was a main factor inducing increased soil C and N accumulation which was related to soil microbial biomass, activity, bacterial community structure and composition.

5. Conclusions

In this study, rotation treatments did not differ in above and below ground biomass input. Thus, increased root diversity, rather than biomass input, mainly drove the crop rotation effect on soil C, N and microorganisms. Our results suggest that increased root diversity through rotation increased C accumulation rate in both legume-cereal and cereal-cereal rotation soils, and increased N accumulation rate in legume-cereal rotation soils. Thirty-year crop rotation regimes increased bacterial abundance and altered bacterial community structure but had no effect on bacterial diversity. Results of this study suggest that increased root diversity through rotation has positive impacts on C and N in soil and promotes bacterial communities with high C and N use efficiencies. This is probably the first report describing a significant effect of long-term root diversity on soil bacterial communities associated with soil C and N accumulation using high-throughput sequencing. Moreover, as an important player in soil C cycle, soil fungi may also contribute to C accumulation and is needed further study.

Conflict of interest

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.geoderma.2017.01.014.

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