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Conservation tillage enhances the stability of the rhizosphere bacterial community responding to plant growth

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Abstract Soil microbes play important roles in plant growth and nutrient cycling. Conservation tillage is extensively used in northern China, which alters the soil structure and nutrient conditions, causing changes in the soil microbial community. However, the influence of conservation tillage on rhizosphere bacteria during plant growth, and associations with plant root nutrient efficiency, and plant productivity remains unclear, particularly regarding the effects on the stability of the soil bacterial community that modifies plant growth. Therefore, the aim of this study was to evaluate the contributions of conservation (chisel plow, zero) tillage and conventional (plow) tillage on the soil rhizosphere bacterial community throughout plant growth. The responses and succession of the bacterial community in the rhizosphere of winter wheat crops growing under conservation and conventional tillage practices were determined through high-throughput sequencing of 16S rRNA. The response of plant growth was determined by measuring plant carbon and nitrogen accumulation from the wheat tillering stage to the flowering stage. Here, we show that variations in rhizosphere alpha and beta diversity throughout plant growth had the greatest contributions to distinguishing conventional plow tillage from conservation (chisel plow, zero) tillage. Additionally, zero tillage (dissimilarity: 11.3%) had less of an effect on the relative abundances of Proteobacteria (Alpha-, Beta-, Gamma-) and Bacteroidetes in the rhizosphere in response to plant growth as compared with plow tillage (dissimilarity: 21.7%). This is the first in-depth study of the effects of conservation and conventional tillage on the stability of rhizosphere bacterial community in response to plant growth. Furthermore, our study indicates that conservation tillage can modify the soil conditions and preserve rhizosphere bacterial memberships. The consequent enhanced stability of the plant growth-promoting rhizobacteria population can help to establish a profitable agroecosystem to in turn enhance soil nutrient conditions and improve plant production sustainably.

Keywords Conservation tillage · Stability · Rhizosphere · Bacterial community · Plant growth

1 Introduction

Soil, as a critical and dynamic regulatory medium, contributes to a large number of biological processes in both natural and managed ecosystems (Barrios 2007). The soil environment harbors the greatest biodiversity found in agroecosystems, and the soil biota provides essential ecosystem services that impact soil nutrient cycling, water transfer, and crop growth, contributing to sustainable soil productivity (Roger-Estrade et al. 2010). In particular, soil determines the resistance and resilience of agroecosystems to mechanical impacts (e.g., soil compaction and tillage) and chemical stresses (e.g., plant protection measures). Agricultural management measures, particularly tillage practices, affect soil biodiversity by inducing biophysical and biochemical changes in the soil. Tillage disturbs soil structure heterogeneity, thereby affecting the relative population size and diversity of dominant soil microbial species that lead to changes in the relationships among the members of the soil biota within the soil ecosystem (Altieri 1999).

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In general, different soil microbial communities respond to variations in tillage intensity in different ways, resulting in differences in soil ecology. This in turn contributes to variation in soil microbial stability when responding to abiotic disturbance and stress.

Rhizosphere microbes live both within and on plant roots and utilize the substrates from the roots in the soil; thus, colonization of the rhizosphere is important for nutrient cycling, plant health, and productivity (Philippot et al. 2013). Root activities shape the soil microbial community by modifying the surrounding soil's physicochemical properties. Dominant factors influencing rhizosphere microbes include the ability to bind to roots, plant age, and plant genotype (Donn et al. 2015). With plant growth, specific compounds and phytochemicals in root exudates differentially affect the diversity and structure of the rhizosphere microbial community at different stages (Huang et al. 2014). In return, plant growth-promoting rhizobacteria specifically and effectively colonize the soil surrounding the roots of plants, which maximizes plant nutrient uptake, promotes plant growth, and confers resistance to abiotic stress (Pii et al. 2015). Given this important ecological interaction, agricultural treatments can alter the essential rhizosphere processes that control nutrient transformation and efficient nutrient acquisition and use, causing changes to crop productivity (Shen et al. 2013).

In the dryland regions of northern China, farming development is constrained by adverse weather, topography, and water resource conditions, as well as the low fertility of the soils coupled with poor soil management (Wang et al. 2007). Adoption of conservation tillage as an alternative to traditional tillage can improve the soil moisture content to various degrees (3–50%), reduce wind erosion, and increase crop yield (8–35%) and water-use efficiency, while saving energy and labor input (greater than 60%), especially during the dry period, where the increase in the crop output was more significant (4–22%) (Zhang et al. 2012). However, only a few studies have evaluated the effect of conservation tillage on the rhizosphere microbial community due to alterations in carbon substrate utilization (Kong and Six 2012; Yang et al. 2013). Our previous study indicated that conservation tillage altered the soil bacterial diversity and functional bacterial composition due to modifications of the soil clay fraction and nutrient conditions (Wang et al. 2016b). However, these previous studies only focused on unique bulk soil bacteria and thus could not clearly and accurately delineate the differential effects of conservation and conventional tillage practices on the rhizosphere microbiota. Therefore, knowledge of how conservation tillage influences the rhizosphere bacterial community at different plant growth stages is currently limited.

To address this gap and provide insight for improving soil management in sustainable agroecosystems, we monitored the responses and succession of the bacterial community in the rhizosphere of winter wheat growing under conservation and conventional tillage practices. Chisel plow and zero tillage are widely used conservation tillage practices, and plow tillage is a conventional tillage practice primarily used in dryland regions of northern China. We distinguished tillage practices with respect to the degree of soil disturbance (plow tillage > chisel plow tillage > zero tillage) by quantifying the fractal characterization of soil aggregation and fragmentation (Perfect and Blevins 1997). The diversity and composition of both the rhizosphere and bulk soil bacterial community were analyzed using Illumina MiSeq sequencing of 16S rRNA gene amplicons. We evaluated the plant carbon and nitrogen accumulation from the wheat tillering stage to the flowering stage, representing the beginning and end of the plant growth period (Meng et al. 2013; Semenov et al. 1999). Overall, the objectives of this study were to (1) determine the dynamic changes in soil bacteria diversity and composition to establish the influence of pulse disturbances caused by tillage practices on community stability and (2) evaluate how the effects of different tillage practices on the rhizosphere bacterial community influence plant resource acquisition and productivity.

2 Materials and methods

2.1 Study site

This study was performed at Northwest A&F University, Yangling, Shaanxi, China (34° 17′ N, 108° 04′ E), at an elevation of 521 m above sea level. The mean annual precipitation in the region is 633 mm, with an average yearly temperature of 13.2 °C (range, 10.4–20.8 °C). The experimental area is in the Guanzhong Plain, which belongs to the drylands of northern China, on the site of a long-term trial that began in 2009. Before 2009, the experimental area was managed using rotary cultivation. The average application rates of N and P for winter wheat were 316 and 163 kg ha^{-1}, respectively, in this region. In our study, base fertilizer was spread evenly over the topsoil at 300 kg N ha^{-1} (from urea) and 120 kg P ha^{-1} (from calcium phosphate) for all tillages at the time of soil preparation. Winter wheat (*Triticum* sp. cv. Shaanmai 139) was sown over the residues of maize (*Zea mays* cv. Shaandan 609) on October 18, 2014, using wheat drills. This area is rain-fed, and no irrigation is applied during either maize or wheat growth.

2.2 Tillage treatment and soil sampling

Experimental treatments combined three tillage methods and residue retention in croplands with a wheat–maize rotation. The main characteristics of conservation (chisel plow and zero) and conventional (plow) tillage treatments (Fig. 1) are

described previously in detail (Wang et al. 2016a). In brief, after the application of fertilizers, a chisel plow, with a depth of 30–35 cm deep with tines 40 cm apart, was used once. Plow tillage was used to plow up the soil to 20–30-cm depths using a moldboard plow, followed by a rotavator for the final seed-bed preparation. Zero tillage involves limited disturbance; however, in order to ensure germination, we adopted rotary tillage at 0–5 cm.

Sampling was conducted during two different stages of winter wheat growth (Fig. 1): the tillering stage (collected on November 21, 2014) and the flowering stage (collected on May 2, 2015). For each sample of rhizosphere soil, five randomly selected wheat plants were harvested as a plot composite rhizosphere sample, and the roots were shaken vigorously to remove soil that was not tightly adhering to the roots (Smalla et al. 2001). Bulk soil was collected away from the root and up to surface a depth of 20 cm. Both the rhizosphere and bulk soil samples were sieved through a 2-mm mesh to eliminate large rocks and roots. Each composite soil sample was homogenized and stored at 4 °C for less than 24 h before DNA extraction.

2.3 Soil physicochemical analysis

The physical and chemical analyses of the soil were performed in the laboratory. Measurements of pH, soil organic carbon, total nitrogen, and soil texture were performed as described in Zhao et al. (2014) and related references within. Soil concentrations of inorganic nitrogen (NH_4 and NO_3), dissolved organic carbon, and dissolved organic nitrogen were determined using the procedure described by Berthrong et al. (2013). Soil moisture was measured gravimetrically. Urease and invertase activities were assayed in 5 g of soil after adding an appropriate substrate and incubating for 24 h at 37 °C and at the optimal pH for each enzyme type, as described by Gu et al. (2009).

2.4 DNA extraction and Illumina sequencing

Microbial DNA was extracted from 1 g of fresh soil three times (for a total of 3 g of soil) using an E.Z.N.A. Soil DNA kit (Omega Bio-Tek, Inc., Norcross, GA, USA) according to the manufacturer's instructions. The concentration and quality of the DNA were assessed using a NanoDrop2000
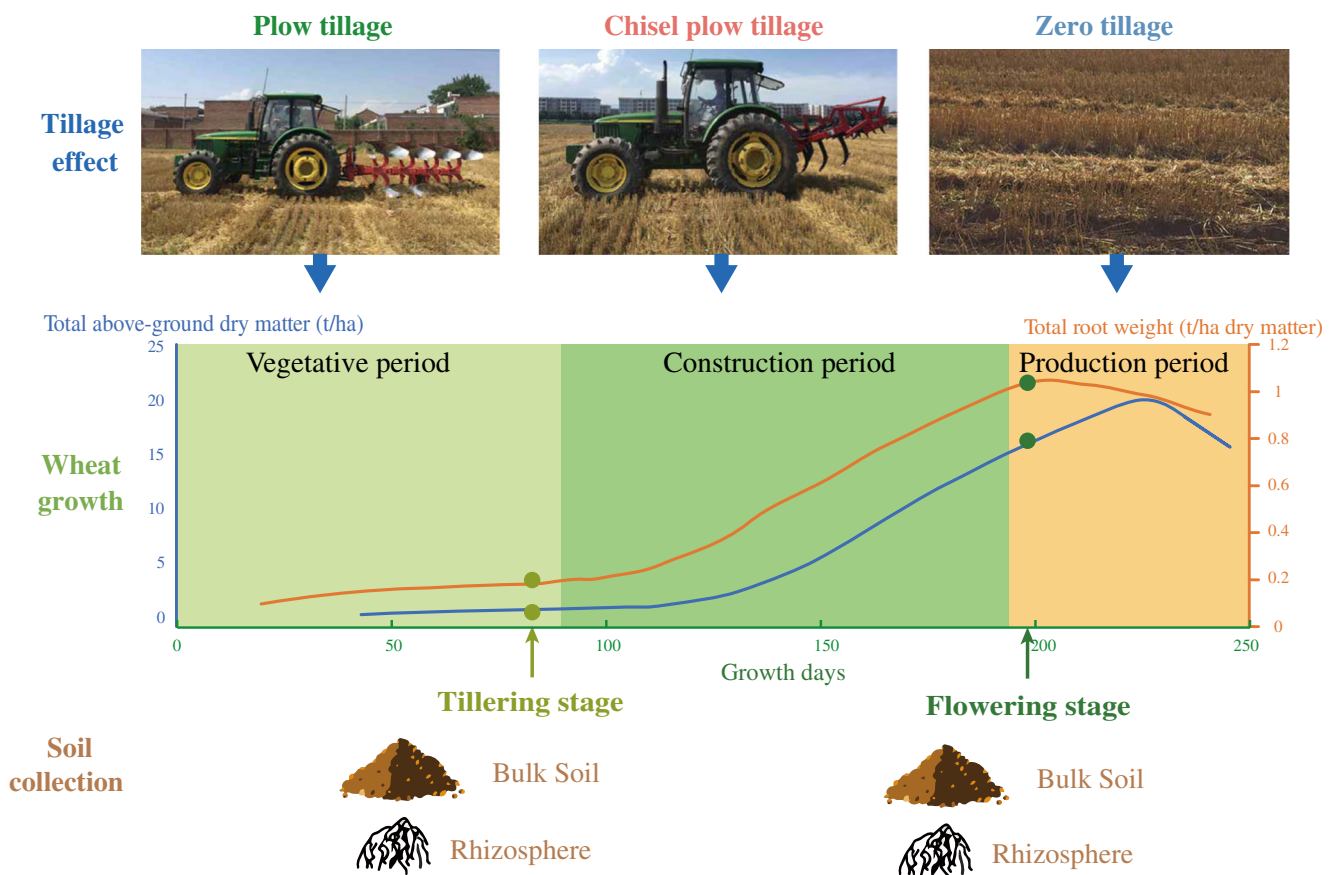

Fig. 1 Conservation (chisel plow, zero) tillage and conventional (plow) tillage applied to the experimental field and experimental design for analysis. Changes in dry matter weight and root weight over the wheat-growing season are shown based on general winter wheat growth data (Agriculture in Arid Regions of China, Wang LX, 2009). The vegetative period starts from sowing and lasts through to the start of stem extension. The construction period starts from the first node being detectable through to flowering. The production period starts just past flowering, lasting through to the grain filling and ripening stage

spectrophotometer (Thermo Scientific, Wilmington, DE, USA). Primers F515 (5′-GTG CCA GCM GCC GCG GTA A-3′) and R806 (5′-GGA CTA CHV GGG TWT CTA AT-3′) targeting the V4 region of the 16S rRNA gene were used for PCR (Peiffer et al. 2013). This primer set provides comprehensive coverage with the highest taxonomical accuracy for bacterial sequences. The reverse primer also contained a 6-bp error-correcting barcode unique to each sample. PCR amplification of the 16S rRNA gene was performed as described previously (Caporaso et al. 2010). Each PCR product was subjected to pyrosequencing by TinyGene Bio-Tech (Shanghai) Co. Ltd. (Shanghai, China) using the Illumina MiSeq platform.

FLASH software was used to merge pairs of reads from the original DNA fragments (Caporaso et al. 2010). Further sequence analysis was performed using USEARCH v5.2.32 to filter and eliminate noise from the data by clustering sequences that were more than 97% identical, and Quantitative Insights Into Microbial Ecology pipeline software was used to select 16S rRNA operational taxonomic units from the combined reads (Edgar 2010). The 16S rRNA gene sequences obtained in this study have been deposited in the NCBI Sequence Read Archive (SRA) database with accession number SRP080901.

2.5 Plant carbon and nitrogen accumulations

In this study, we collected 15 plant samples for each tillage practice at the tillering and flowering stage, drying under 105° for 30 min, and the dry matter weight was determined after drying under 80 °C for 24 h. The total carbon content of the plants was determined by the $K_2Cr_2O_7$ capacity method, and the total nitrogen content of the plants was determined by the Kjeldahl method. Plant carbon accumulation (total carbon content × dry matter weight) and nitrogen accumulation (total nitrogen content × dry matter weight) were estimated (Uhart and Andrade 1995).

2.6 Statistical and bioinformatics analysis

Alpha diversity was estimated using the Shannon diversity index and Simpson diversity index. Estimation of the beta diversity and phylogenetic community comparisons were performed using weighted and unweighted UniFrac distance matrices. Taxonomic compositions were determined based on the relative abundances of dominant phyla and four classes of Proteobacteria. Correlations between the soil bacterial community structure and soil characteristics were determined using Mantel tests with 999 permutations.

All statistical analyses and Spearman's rank correlations between abundant phyla and soil properties were conducted using SPSS 22.0 (SPSS Inc., Chicago, IL, USA). Analyses involving

Fig. 2 a The rhizosphere–bulk and plant-stage variations of bacterial diversity under three tillage practices, and the Pearson correlation coefficient between diversity and soil properties. V: variations, TB: bulk soil at the tillering stage, TR: rhizosphere at the tillering stage, FB: bulk soil at the flowering stage, FR: rhizosphere at the flowering stage. The lengths in cells represent the value of variations (legend of Shannon' diversity between 0 and 0.796; legend of Simpson' diversity between 0 and 0.014; legend of phylogenetic membership between 0 and 0.187; legend of phylogenetic composition between 0 and 0.176). Plow tillage (green lines); zero tillage (blue lines); chisel plow tillage (red lines). **b** Principal coordinate analysis of soil characteristics (arrows), including soil clay, silt, sand fraction, soil organic carbon (SOC), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), total nitrogen (TN), NH_4, NO_3, urease, and invertase, of different soil types from different tillage treatments. The x-axis distinguishes the difference of soil nutrients between the rhizosphere (positive axis) and bulk soil (negative axis), and the y-axis distinguishes soil nutrient status under conservation (chisel plow, zero) tillage (positive axis) and conventional tillage (negative axis). The length and direction of the different arrows of nutrients indicate the effect of nutrient differences on each treatment. Plow tillage (green circles); zero tillage (blue squares); chisel plow tillage (red triangles)

weighted and unweighted UniFrac distances, similarity percentage analysis, and Mantel tests were performed using the "vegan" package in the R v3.20 statistical environment. $P < 0.05$ was considered statistically significant.

2.7 Measurement of soil bacterial community ability

Ecosystem ability is defined as the system's ability to minimize dynamic undulation and the ability to resist changes (McCann 2000). In this study, differences in a given soil type (rhizosphere or bulk soil) between the tillering and flowering stages were considered to represent growth-stage variation in the soil bacterial community, whereas differences between the rhizosphere and bulk soil at the same plant growth stage (tillering or flowering) were considered to represent rhizosphere-bulk variation in the soil bacterial community (Fig. 1). We measured these variations to determine the stability of the soil bacterial community under conservation (chisel plow, zero) and conventional (plow) tillage treatments.

The formulas for calculating the two types of variation are as follows:

$$\Delta v_{TB-FB} = \left| v_{Tillering \cdot Bulk} - v_{Flowering \cdot Bulk} \right| \tag{1}$$

$$\Delta v_{TR-FR} = \left| v_{Tillering \cdot Rhizosphere} - v_{Flowering \cdot Rhizosphere} \right| \tag{2}$$

$$V_{growth-stage} = \Delta v_{TB-FB} + \Delta v_{TR-FR} \tag{3}$$

$$\Delta v_{TR-TB} = \left| v_{Tillering \cdot Rhizosphere} - v_{Tillering \cdot Bulk} \right| \tag{4}$$

$$\Delta v_{FR-FB} = \left| v_{Flowerin \cdot Rhizosphere} - v_{Flowering \cdot Bulk} \right| \tag{5}$$

$$V_{Rhizosphere-Bulk} = \Delta v_{TR-TB} + \Delta v_{FR-FB} \tag{6}$$

a) Relationships between bacterial diversity and soil properties

Bacterial diversity	V_{TB-FB}	V_{TR-FR}	V_{TB-TR}	V_{FB-FR}	Clay	Silt	Sand	SM	pH	DOC	DON	SOC	TN	NO_3	NH_4	Invertase	Urease
Shannon' diversity	0.031	0.109	0.547	0.468	0.809	0.682	0.930	0.215	0.944	0.793	0.197	0.243	0.795	0.847	0.926	0.861	0.517
	0.085	0.458	0.795	0.408	0.762	0.565	0.735	0.067	0.749	0.684	0.063	0.512	0.119	0.818	0.783	0.893	0.845
	0.076	0.117	0.361	0.353	0.720	0.403	0.864	0.241	0.872	0.839	0.048	0.198	0.724	0.918	0.917	0.880	0.807
Simpson' diversity	0.000	0.003	0.006	0.003	0.731	0.539	0.793	0.066	0.810	0.666	0.316	0.015	0.688	0.700	0.780	0.765	0.650
	0.001	0.012	0.014	0.003	0.510	0.441	0.527	0.248	0.553	0.559	0.180	0.121	0.211	0.638	0.584	0.734	0.634
	0.000	0.002	0.005	0.003	0.572	0.565	0.873	0.105	0.871	0.845	0.157	0.138	0.752	0.810	0.883	0.835	0.768
Phylogenetic membership	0.072	0.119	0.142	0.154	0.392	0.069	0.154	0.089	0.140	0.015	0.171	0.290	0.059	0.399	0.227	0.509	0.380
	0.093	0.176	0.187	0.165	0.463	0.010	0.433	0.346	0.533	0.363	0.021	0.000	0.457	0.575	0.534	0.552	0.212
	0.071	0.112	0.137	0.129	0.528	0.038	0.186	0.115	0.261	0.311	0.180	0.388	0.279	0.459	0.287	0.419	0.197
Phylogenetic composition	0.145	0.160	0.155	0.150	0.442	0.261	0.779	0.431	0.820	0.420	0.044	0.115	0.394	0.653	0.808	0.576	0.260
	0.149	0.176	0.175	0.168	0.488	0.205	0.405	0.183	0.393	0.232	0.244	0.372	0.009	0.525	0.471	0.617	0.552
	0.167	0.161	0.159	0.159	0.322	0.251	0.793	0.326	0.801	0.736	0.125	0.124	0.511	0.766	0.841	0.686	0.479

b) PCoA of soil properties
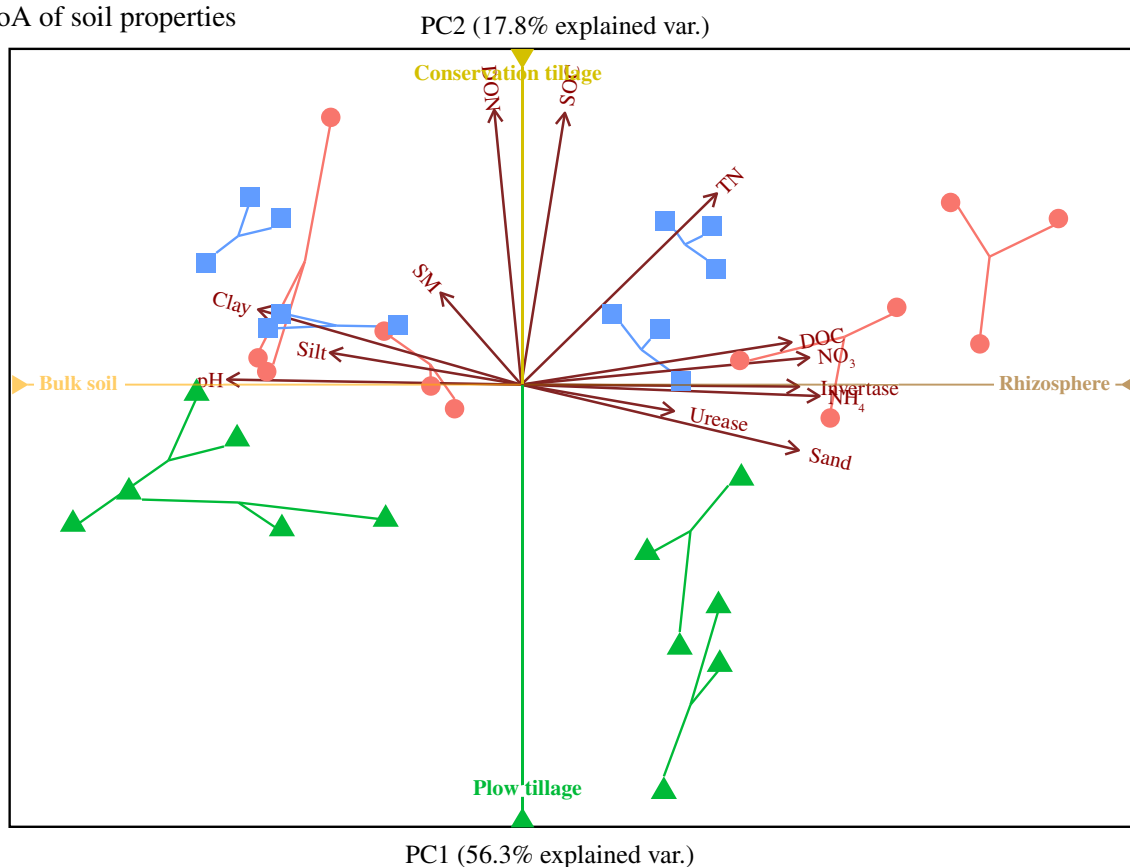
where v refers to the value of the soil bacterial community (including bacterial diversity and taxonomic composition), Δv refers to differences in the soil bacterial community at different stages or different soil collecting types, and V refers to variation in the soil bacterial community (including bacterial diversity, community abundance, and taxonomic composition) caused by different plant growth stages or different soil types.

3 Results and discussion

3.1 Stability of soil bacterial diversities

In our study, we used the Shannon and Simpson indices to determine the influence of different tillage practices on bacterial alpha diversity. For all tillage practices, the rhizosphere-bulk variation in alpha diversities (0.489) was greater than the plant growth-stage variation (0.127) (Fig. 2a). The rhizosphere showed higher available nutrients (dissolved organic carbon, inorganic nitrogen) and enzyme activities (invertase, urease) compared to those of the bulk soil (Fig. 1b), indicating more active exchange of substances and energy flow processes in the rhizosphere bacteria compared to those of the bulk soil (Hinsinger et al. 2009). Alpha diversity patterns also varied among the three tillage practices (Fig. 2a). As compared to chisel plow and zero tillage, plow tillage caused greater rhizosphere-bulk variations for both the Shannon and Simpson indices at the tillering stage, resulting in increased plant growth-stage variations in the rhizosphere (Fig. 2a). Especially, zero tillage had the lowest contribution to rhizosphere-bulk variations in alpha diversities and their effect on plant growth-stage variations (Fig. 2a). Moreover, both the Shannon and Simpson indices had different relationships with soil properties among the three tillage practices (Fig. 2a). The soil sand fraction and pH were major factors driving variations of alpha diversities under chisel plow and zero tillage, and soil enzyme activities (invertase and urease) and inorganic nitrogen had stronger impacts on the variations in diversity under plow tillage (Fig. 2a). Our results also showed that conservation (chisel plow, zero) tillage resulted in a higher soil nutrient status and distinct soil structure from plow tillage (Fig. 2b, Table 1). These unique edaphic environmental properties can contribute to variations in the degree to which bacterial communities respond to changes of biotic and abiotic factors (de Vries and Shade 2013; Hallett et al. 2014). Compared to conservation tillage, the lower inorganic nitrogen and enzyme activities under plow tillage would limit the ability of soil bacteria to acquire a sufficient amount of nutrients, thereby increasing the sensitivity of bacterial alpha diversity in response to environmental changes (Kivlin and Hawkes 2016).

For measuring bacterial beta diversity, we used unweighted and weighted UniFrac distances to perform phylogenetic analysis of community membership and composition, respectively. In general, plant growth increased the variations of bacterial beta diversity in the rhizosphere as compared to the bulk soil, and we found higher rhizosphere-bulk variations among the three tillage practices (Fig. 2a). Plant growth stage and plant species regulate root exudates, causing changes of available nutrients to discriminate rhizosphere bacterial phylogenetic membership and composition from those of the bulk soil (Haichar et al. 2008). Indeed, in the present study, the different tillage practices induced variations in the patterns of beta diversity in response to plant growth (Fig. 2a). Compared with chisel plow and zero tillage, plow tillage showed higher variations in both phylogenetic membership and composition (Fig. 2a). Mantel analysis also revealed that different soil properties contributed to the rhizosphere-bulk variations in beta diversity and the response during plant growth (Fig. 2a). Zero tillage showed the lowest variations of both rhizosphere-bulk and plant growth stage in bacterial beta diversity among the three tillage practices, which can be explained by the stronger relationships between beta diversity and most of the soil properties measured (Fig. 2a). A previous study demonstrated that zero tillage, as a practice to minimize soil disturbance, could increase the soil organic matter and improve soil structure, and thereby result in better aeration and water contents due to enhancing the heterogeneity of the soil microbiota (Borie et al. 2006). In this study, zero tillage resulted in higher soil carbon contents (soil organic carbon, dissolved organic carbon; Fig. 2b), which was closely related to higher invertase activity and fine clay fractions (Berthrong et al. 2013). This can establish a more favorable microclimate (typically cooler and moister soil conditions), thus improving soil bacterial community resistance and resilience (Zuber and Villamil 2016). In contrast, plow tillage decreased the available nutrients (inorganic nitrogen contents) and enzyme activities owing to the more intensive soil disturbance (Fig. 2b). This would increase the sensitivity of the soil bacterial diversity to changes of soil nutrient content along with changes in plant growth, thereby enhancing the growth-stage variations of bacterial beta diversity in the rhizosphere soil (Li et al. 2014).

In particular, we observed that the plant growth-stage variations in bacterial diversity was the major contributor to distinguishing plow tillage from conservation (chisel plow, zero) tillage. During the root growth of a plant, the exudates support various easily utilized chemical compounds that act as drivers of rhizosphere bacterial diversity at the flowering stage, resulting in a difference from the tillering stage (Chaparro et al. 2014). Rhizosphere microbes have evolved intimate relationships with plants, and rhizosphere soil microbes modulate soil properties to mediate and influence the various factors that contribute to plant productivity (Chaparro et al. 2012). In this study, we found that plant nitrogen and carbon accumulation had a significantly negative correlation to growth-stage variations in rhizosphere bacterial beta diversity (Fig. 3). Additionally, bacterial phylogenetic membership and composition were both distinct according to tillage practice ($R^2 = 0.245$, $p = 0.001$ and $R^2 = 0.406$, $p = 0.001$, respectively) due to the influence of soil clay fractions ($R^2 = 0.118$, $p = 0.001$ and $R^2 = 0.178$, $p = 0.001$, respectively), soil moisture ($R^2 = 0.115$, $p = 0.001$ and $R^2 = 0.173$, $p = 0.001$, respectively), and organic carbon ($R^2 = 0.073$, $p = 0.049$ and $R^2 = 0.146$, $p = 0.001$, respectively). Zero tillage is more conducive to development of the soil structure for enhancing

Table 1 Soil physical–chemical properties and plant nitrogen/carbon accumulation among treatments

Tillage	Treatment[a]	Clay (%)	Silt (%)	Sand (%)	SM (%)	pH	DOC (mg/kg)	DON (mg/kg)	SOC (g/kg)	TN (g/kg)	NO$_3$ (mg/kg)	NH$_4$ (mg/kg)	Urease (mg/g)	Invertase (mg/g)	Plant accumulation N (kg/ha)	C (kg/ha)
Chisel plow tillage	TR	29.7 b[b]	61.4 ns	8.88 ns	17.3 a	7.99 b	42.2 ns	20.8 b	8.327 a	1.345 a	17.45 a	4.87 ns	12.986 ns	13.924 ns	55.1 b	78.9 a
	TB	34.2 ns	61.7 ns	4.10 ns	17.0 a	8.14 ns	33.4 ns	23.1 a	9.293 a	0.809 ns	9.64 ns	1.47 ns	8.225 ns	3.743 a		
	FR	29.3 b	60.3 b	10.44 a	11.4 ns	7.95 c	45.9 ns	22.1 a	10.401 a	1.483 a	20.64 a	6.12 a	9.333 b	15.338 a	144.6 b	2908.5 a
	FB	31.5 c	64.9 ns	3.53 a	14.9 ns	8.12 c	35.0 ns	20.8 ns	8.345 ns	1.059 ns	13.52 a	2.06 a	9.420 ab	8.796 a		
	Variations[c]	9.83 a	10.42 a	14.32 a	0.12 a	0.38 a	30.5 ab	7.84 a	6.23 a	1.42 a	22.00 a	9.32 a	11.08 b	23.25 a	89.5 b	2829.5 a
Plow tillage	TR	30.7 b	61.3 ns	8.03 ns	15.6 b	8.05 a	40.9 ns	20.2 b	6.564 b	0.797 b	15.29 b	3.82 ns	16.908 ns	13.295 ns	51.6 b	65.5 b
	TB	33.4 ns	62.5 ns	4.12 ns	15.8 b	8.14 ns	32.0 ns	19.4 b	7.164 b	0.760 ns	10.51 ns	0.57 ns	7.802 ns	2.880 b		
	FR	30.2 ab	61.1 ab	8.70 a	11.8 ab	8.04 b	42.1 ns	17.4 b	6.219 c	0.795 c	15.45 c	4.11 b	11.633 ab	11.069 b	135.9 c	2517.0 b
	FB	34.0 a	64.7 ns	1.30 b	14.2 ns	8.19 a	26.7 ns	20.5 ns	7.500 ns	0.785 ns	9.38 b	1.38 b	8.116 ns	5.307 c		
	Variations	8.05 a	8.88 ab	15.17 a	0.08 b	0.31 b	35.1 a	8.00 a	3.05 b	0.61 b	12.84 b	7.26 b	19.36 a	20.87 b	84.3 c	2451.5 b
Zero tillage	TR	32.2 a	61.3 ns	6.55 ns	17.8 a	8.05 a	43.6 ns	23.6 a	8.749 s	1.256 a	16.25 ab	3.78 ns	15.150 ns	13.458 ns	57.8 a	78.5 a
	TB	34.8 ns	63.0 ns	2.21 ns	16.4 ab	8.16 ns	33.2 ns	23.5 a	9.159 s	1.037 ns	10.20 ns	1.04 ns	8.744 ns	3.456 a		
	FR	31.2 a	63.7 a	5.10 b	11.8 ns	8.08 a	40.9 ns	22.5 a	8.364 b	1.197 b	17.01 b	3.35 c	14.744 a	12.560 b	149.5 a	2961.3 a
	FB	32.8 b	65.2 ns	1.95 b	14.6 ns	8.16 a	32.4 ns	22.5 ns	8.432 ns	0.987 ns	12.39a	1.25 b	11.522 ns	7.523 b		
	Variations	7.55 a	7.89 b	9.66 b	0.12 a	0.24 c	24.2 b	4.90 b	2.08 b	0.62 b	13.66 b	5.61 c	14.94 b	20.00 b	91.7 a	2882.7 a

SM Soil moisture, *DOC* dissolved organic carbon, *DON* dissolved organic nitrogen, *SOC* soil organic carbon, *TN* total nitrogen, *TR* tillering·rhizosphere, *TB* tillering·bulk, *FR* flowering rhizosphere, *FB* flowering bulk

[a] Values are mean of three soil samples

[b] Different letters indicate significant differences (ANOVA, $P < 0.05$, Tukey's HSD post hoc analysis) among three tillage practices

[c] Variations (soil properties) = $V_{growth\text{-}stage}$ + $V_{rhizosphere\text{-}bulk}$; Variations (plant N/C accumulation) = $V_{growth\text{-}stage}$

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a) Plant nitrogen accumulation

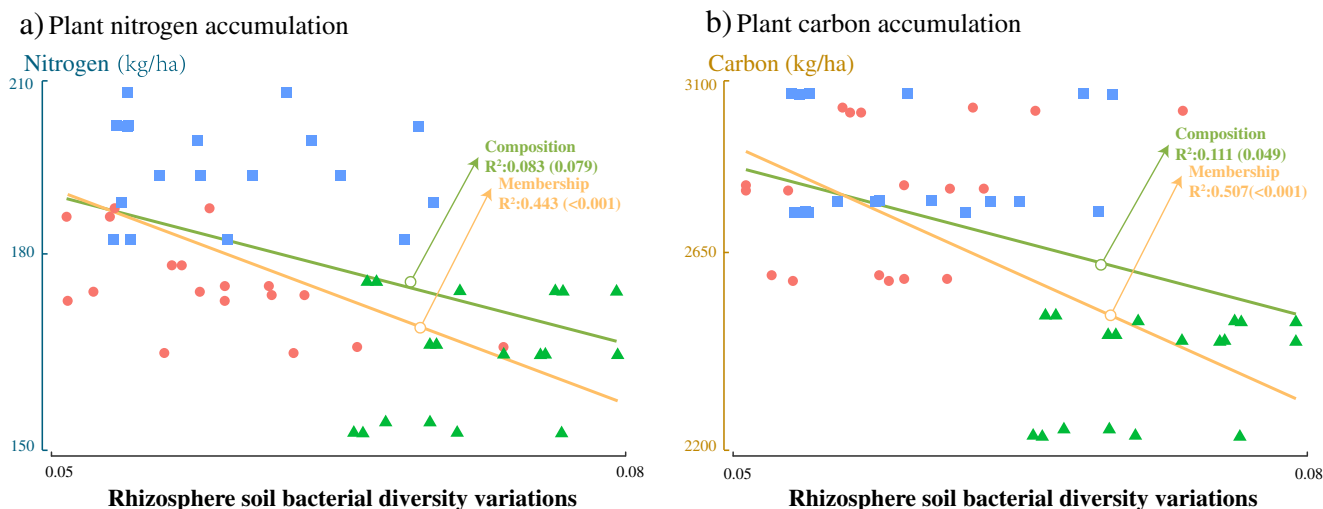b) Plant carbon accumulation

Fig. 3 Regression analysis to explore the relationship between beta diversity and plant **a** carbon or **b** nitrogen accumulation increments. The x-axis indicates the variation of the rhizosphere bacterial composition and membership, and the y-axis indicates the accumulation of plant carbon and nitrogen. Plow tillage (*green triangles*); zero tillage (*blue squares*); chisel plow tillage (*red circles*)

bacterial diversity, whereas plow tillage results in breaking up of micro-sites to alter microbial interactions, leading to soil compaction, erosion, a reduced pore volume, and desiccation (Lupwayi et al. 2012). Plant nitrogen and carbon accumulation increased along with a decrease in the variations of rhizosphere bacterial membership, which was attributed to moderate soil disturbance (Fig. 3). Furthermore, higher levels of available nutrients in the soil (total nitrogen, dissolved organic carbon, inorganic nitrogen) and enzyme activity separated conservation (chisel plow, zero) tillage from plow tillage (Fig. 2b). The stability of phylogenetic membership revealed that the members of the root microbiota under zero tillage appear to have common host functions for acquiring nutrients from the soil to enhance plant growth (Bulgarelli et al. 2013). There was much greater variation in the rhizosphere bacterial species under plow tillage, which were considered to be closely linked to organic carbon mineralization resulting in relatively low invertase activity and organic carbon contents in the roots surrounding the soil (Fig. 2b), thereby reducing the ability for plant nutrient acquisition (Nannipieri et al. 2008). Overall, conservation tillage, as a practice resulting in less soil disturbance, can help to preserve the soil structure and enhance soil nutrient states, thereby contributing to stable rhizosphere bacterial diversity and composition; the function of these bacteria can then feedback to help maintain agrobiodiversity and enhance plant growth through facilitating nutrient acquisition.

3.2 Stability of soil bacterial taxonomic composition

Our analysis of all soil samples yielded a total of 1,052,791 high-quality sequences with a mean of 23,396 sequences per sample. Of the total sequences, 99.8% were classified in the

bulk soil and 99.6% were classified in the rhizosphere soil. We used non-metric multidimensional scaling to illustrate the clustering of different samples based on Bray-Curtis distances (Fig. 4a). Rhizosphere bacterial taxonomic composition was significantly separated from that of the bulk soil ($R^2 = 0.504$, $p = 0.001$) due to the enriched relative abundance of the major phyla Actinobacteria (+37.2%) and Bacteroidetes (+94.2%) in the roots surrounding the soil. In addition, soil inorganic nitrogen, sand fractions, dissolved organic carbon, and invertase activity showed strong correlations with the rhizosphere-bulk variations of bacterial taxonomic composition (Fig. 4a). Plant root exudates input chemical compounds into the soil via rhizodeposition, thereby decreasing the value of pH, which in turn significantly increase the abundance of Actinobacteria in the rhizosphere (Marschner et al. 2004). Our result is consistent with a previous study showing that plant roots selectively stimulated the relative abundance of Bacteroidetes, which are copiotrophic soil bacteria that are well adapted to labile substrates and available conditions in the rhizosphere (Goldfarb et al. 2011). The bacterial taxonomic composition showed sharper changes along with plant growth in the rhizosphere (dissimilarity: 15.1%) than in the bulk soil (dissimilarity: 9.1%). We observed that plant growth and root exudation selection increased the relative abundances of Alphaproteobacteria, Betaproteobacteria, and Bacteroidetes but reduced the populations of Gammaproteobacteria, Actinobacteria, and Firmicutes (Fig. 4a). Proteobacteria and Bacteroidetes commonly respond sensitively to plant roots, since these phyla are the major microbial groups utilizing root exudates (DeAngelis et al. 2009). The increasing relative abundances of Alphaproteobacteria, Betaproteobacteria, and Bacteroidetes showed strong and positive relationships with the soil available nutrient content (dissolved organic carbon, dissolved organic nitrogen)

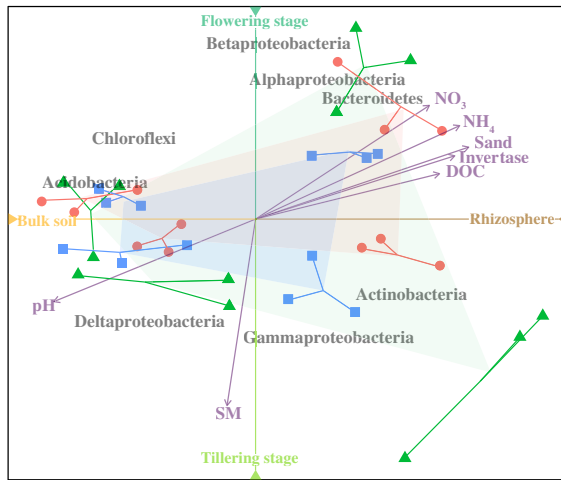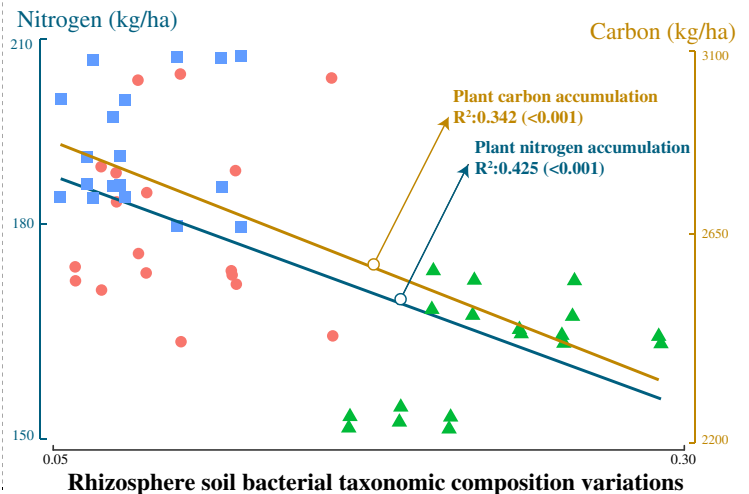a) NMDS of bacterial taxonomic composition

b) Plant nitrogen/carbon accumulation

Fig. 4 a Non-metric multi-dimensional scaling plots of the bacterial communities based on Bray-Curtis dissimilarities and soil characteristics (arrows), including soil clay, silt, sand fraction, soil organic carbon (SOC), dissolved organic carbon (DOC), dissolved organic nitrogen (DON), total nitrogen (TN), NH_4, NO_3, urease, and invertase, of different soil types from different tillage treatments. The x-axis distinguishes the taxonomic composition differences between the rhizosphere (positive axis) and the bulk soil (negative axis). The y-axis distinguishes the bacterial taxonomic composition from the flowering stage (positive axis) and tillering stage (negative axis). The length and direction of the different nutrient arrows indicate the extent to which the treatments are affected by the nutrient differences. **b** Regression analysis to explore the relationship between variations of bacterial taxonomic composition and plant carbon or nitrogen accumulation increments. The x-axis indicates the variation of the taxonomic composition, and the y-axis indicates the accumulation of carbon and nitrogen in the plant. Plow tillage (*green circles*); zero tillage (*blue squares*); chisel plow tillage (*red triangles*)

and enzyme activity at the flowering stage (Fig. 4a). During plant growth, a variety of exudate compounds are released to modify the soil nutrient condition surrounding the roots, thus selecting for or against specific bacterial species populations (Shi et al. 2015).

Importantly, our results showed that the rhizosphere bacterial taxonomic composition responds differently to plant growth stage under conservation (chisel plow, zero) tillage and plow tillage (Fig. 4a). Compared with plow tillage (dissimilarity: 21.7%), the rhizosphere taxonomic composition at the tillering stage was more similar to that at the flowering stage under zero tillage (dissimilarity: 11.3%). These phenomena were explained by the varying degrees of the relative abundances of Proteobacteria (Alpha-, Beta-, Gamma-) and Bacteroidetes (Fig. 4b). Alphaproteobacteria and Betaproteobacteria are generally fast-growing r-strategists with the ability to utilize a wide range of root-derived carbon substrates (Peiffer et al. 2013); thus, the high amounts of dissolved organic carbon and invertase activity under zero tillage contribute to the sustained stability of Proteobacteria in response to plant growth (Fig. 2b). Bacteroidetes are important contributors to nutrient turnover, in that these bacteria contain genes for denitrification, indicating a possible role in nitrogen cycling (Chaparro et al. 2014). Therefore, the lower inorganic nitrogen contents under plow tillage may attenuate nitrogen transport, causing larger variation in Bacteroidetes with plant growth (Table 1). Given that plants

adapt to the physicochemical properties of the rhizosphere soil, thereby selecting for a subset of microbes at different stages of development, the increase in soil condition with conservation tillage that minimizes soil disturbance would help to promote root growth so as to select for favorable bacterial populations (Bulgarelli et al. 2013).

Particularly, our study indicated that variations in the rhizosphere bacterial taxonomic composition are significantly negatively correlated with both plant carbon ($R^2 = 0.342$, $p < 0.001$) and nitrogen ($R^2 = 0.425$, $p < 0.001$) accumulation increments with increasing soil disturbance (Fig. 4b). A number of bacterial species belonging to the phyla Actinobacteria (*Arthrobacter*, average: 6.3%), Alphaproteobacteria (*Azospirillum*, *Alcaligenes*, average: 9.3%), Betaproteobacteria (*Burkholderia*, average: 2.9%), Gammaproteobacteria (*Acinetobacter*, *Enterobacter*, *Pseudomonas*, average: 2.6%), and Bacteroidetes (*Flavobacterium*, average: 0.7%) are associated with the plant rhizosphere and are able to exert a beneficial effect on plant growth (Tilak et al. 2005). These plant growth-promoting rhizobacteria can increase the soil's resistance to pathogen invasion, with benefits of increased yields, nutrient acquisition, stress tolerance, and disease resistance to the plant host (Pii et al. 2015). In this study, the lower variations of plant growth-promoting rhizobacteria along with less soil disturbance distinguished conservation (variation for chisel plow: 2.2%; zero: 1.9%) tillage from plow tillage (variation 4.7%).

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A previous study demonstrated that these mixed microbial growth-promoting biochemical processes increased the plant germination rate, shoot and root length, dry weight, and chlorophyll and nutrient contents, further establishing an environment that is more favorable for plant growth to realize a functional agroecosystem (Lugtenberg and Kamilova 2009). Similarly, in our study, conservation tillage allowed for the stable abundance of plant growth-promoting rhizobacteria that act as biocontrol agents while enhancing nutrient acquisition, thereby modifying the soil nutrients surrounding the roots to ultimately stimulate plant growth (Yuan et al. 2015).

4 Conclusion

In this study, we explored the variations in rhizosphere and bulk soil microbial communities across different stages of plant growth under conservation (chisel plow, zero) tillage and conventional (plow) tillage. Our results highlight that conservation tillage with abundant soil nutrients allows for the establishment of more favorable aeration and water contents, thereby enhancing the stability of rhizosphere bacterial diversity over time in response to plant growth. The variations of Proteobacteria (Alpha-, Beta-, Gamma-) and Bacteroidetes populations along with plant growth could clearly distinguish the rhizosphere bacterial taxonomic composition between conservation tillage and plow tillage. Importantly, we found that plant carbon and nitrogen accumulation increments significantly negatively correlated with variations in rhizosphere bacterial diversity and taxonomic composition responding to plant growth. One of the major conclusions of this study is that conservation tillage, as a moderate disturbance practice, can preserve the soil structure and enhance the soil nutrient status, thereby contributing to a stable rhizosphere phylogenetic diversity and selection for favorable plant growth-promoting rhizobacteria. This established rhizosphere bacterial community can in turn improve root nutrient uptake and accelerate plant growth. Overall, the present analysis allowed for delineating the various interacting factors in a soil ecosystem to provide new understanding as to how conservation practices can establish a profitable agroecosystem for preserving the sustainability of the soil condition and promoting plant productivity. Additional research should focus on the rhizosphere fungal community, especially mycorrhizal fungi that strongly associate with plant roots and draw nutrients from the soil.

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