Plant Soil
https://doi.org/10.1007/s11104-022-05457-7

RESEARCH ARTICLE

Nitrogen application increases soil microbial carbon fixation and maize productivity on the semiarid Loess Plateau

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Received: 31 October 2021 / Accepted: 22 April 2022

Abstract

Background and aims Soil autotrophic microorganisms and plant primary production play crucial roles in soil carbon (C) cycling. However, the information remains limited to whether and how nitrogen (N) application influences the contribution of soil microbial C fixation to the soil organic C (SOC) pool.

Methods We investigated the effects of soil autotrophic bacterial communities on SOC storage and maize yield. A field experiment was conducted with four application rates of urea on the semiarid Loess Plateau, N application at 0 kg ha^{-1} (N0), 100 kg ha^{-1} (N1), 200 kg ha^{-1} (N2), and 300 kg ha^{-1} (N3), respectively.

Results Our results showed that SOC storage and maize yield were significantly increased by N application, but no significant SOC storage difference between N2 and N3 treatments, no further yield increase beyond 200 N kg ha^{-1} application was observed. N application significantly impacted soil Calvin-Benson-Bassham (CBB) (*cbbL*) gene-carrying bacterial communities via changing soil pH, nitrate N, and soil water content. The diversity of soil autotrophic bacterial communities decreased with increasing rate of N application. We detected a high abundance of the autotrophic bacterial dominant genera *Xanthobacter*, *Bradyrhizobium*, *Aminobacter*, and *Nitrosospira*. The co-occurrence network of autotrophic bacteria contained four distinct modules. Structural equation modeling further indicated that the autotrophic bacterial communities had positive relationships with SOC storage and maize yield.

Conclusions Taken together, our results highlighted that N application stimulated the activity of soil autotrophic bacterial communities, contributing to an increase in SOC. The increase of SOC under N fertilization can stabilize soil fertility for maize production.

Keywords Soil autotrophic bacteria · SOC pool dynamics · Application rates of urea · Maize yield · Semi-arid Loess Plateau

Responsible Editor: Florian Wichern.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s11104-022-05457-7.

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Published online: 29 April 2022

Introduction

Soil organic carbon (SOC) is a key predictor for soil quality and crop production (Wiesmeier et al. 2019). Given that SOC is closely related to crop yield, agricultural system productivity can be enhanced by increasing SOC pool (Yuan et al. 2021a). Agricultural management regimes can drive soil microbial community structure to improve SOC storage through a series of biochemical reactions, including adding soil organic matter to soils (Jiang et al. 2018; Berhane et al. 2020), reducing the decomposition rate of organic matter (Zang et al. 2017), and the combination of these measures. Hitherto, the question remains how the biological mechanisms of soil microbial communities regulate SOC dynamics and crop productivity.

Soil autotrophic bacterial communities play crucial roles in mediating SOC dynamics through catabolism and anabolism (Wang et al. 2021b; Zheng et al. 2021), and indirectly influence soil sustainability and plant productivity (Muhammad et al. 2020). Soil autotrophic bacteria have developed six pathways of carbon dioxide (CO_2) fixation in different terrestrial ecosystems (Berg 2011), with the Calvin-Benson-Bassham (CBB) cycle as the dominant pathway (Yuan et al. 2012a; Qin et al. 2021). In the Calvin cycle, Ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) is responsible for catalyzing the first rate-limiting step of autotrophic CO_2 fixation (Selesi et al. 2005; Yuan et al. 2012a). To date, four RubisCO forms (forms I–IV) have been found to be different in structure, catalytic property, and O_2 sensitivity, with form I of RubisCO as the most abundant among the four forms. The Calvin-Benson-Bassham (CBB) (*cbbL*) gene, which encodes a large subunit of RubisCO I, has been often used as a phylogenetic marker to investigate the autotrophic bacterial communities (Kovaleva et al. 2011). Several studies have supported that fertilization regimes, tillage, and mulching practices have strong impacts on the soil autotrophic bacterial communities and enzyme activities through altering SOC, pH, bulk density, and available phosphorus (Yuan et al. 2012b; Lu et al. 2019; Liao et al. 2020; Wang et al. 2020). However, relatively few of these studies have sought to explore how agronomic practices alter the structure and network of the soil autotrophic bacterial communities.

The Loess Plateau is a very important rainfed food production region in China, and maize (*Zea mays* L.) is one of the dominant crops in this region. N is the important limiting element for maize growth as well as yield (LeBauer and Treseder 2008). Long-term excessive chemical fertilization leads to decline in soil quality, nutrient balance and crop productivity (Shen et al. 2010; Miao et al. 2011; Agegnehu et al. 2016). Appropriate N fertilizer application can not only improve N utilization efficiency and reduce the waste of fertilizer resources (Zhang et al. 2015; Wang et al. 2019), but also promote SOC and crop productivity via regulating soil autotrophic bacterial communities (Liao et al. 2020; Wang et al. 2021a). However, the information remains limited regarding how long-term N fertilization affects the activity of soil autotrophic bacterial communities, which facilitates SOC accumulation on the semiarid Loess Plateau.

Here, we performed an 8-year field experiment with four N fertilizer application rates on the semiarid Loess Plateau and evaluated the importance of soil autotrophic bacterial communities on SOC, and that of SOC on maize productivity under field conditions since SOC is important for stabilizing soil fertility. We asked the following two questions: (1) How does the composition and co-occurrence network of soil autotrophic bacterial communities respond to four N fertilizer treatments? (2) How does the soil autotrophic bacterial communities contribute to the SOC dynamics, beneficial for maize productivity?

Materials and methods

Field experiment description

The long-term N fertilization experiment was conducted at the Rainfed Agricultural Experimental Station of Gansu Agricultural University (35°28'N, 104°44'E) in Gansu province, China. The experiment site is located in a warm temperate zone with a continental monsoon climate, with mean annual temperature of 6.4℃ and mean annual precipitation of 390 mm. The soil is classified as Calcaric Cambisol according to the Food and Agricultural Organization (FAO) classification system. The long-term field experiment used a randomized complete block design with three replications. The four application rates of N fertilizers at 0 kg ha^{-1} (N0), 100 kg ha^{-1} (N1),

200 kg ha^{-1} (N2), and 300 kg ha^{-1} (N3), respectively, were applied randomly in each block. (Fig. S1). The experiment was started in 2012, which consisted of 12 plots. N fertilizer was applied as urea (46% N) in two splits: one-third was broadcast on the soil surface and incorporated by moldboard plowing into soil and the remaining two-thirds was applied at jointing stage of maize. Triple superphosphate (P_2O_5 16%) was applied at 150 kg P_2O_5 ha^{-1}, and was evenly broadcast on the soil surface of all plots.

The experimental plots were 18.7 m^2 (4.25 m length and 4.4 m width) and consisted of narrow ridges (15 cm height and 40 cm width) alternated with wide ridges (10 cm height and 70 cm width). All ridges were covered by the plastic film (0.01 mm thickness and 140 cm width). Maize monoculture (cv. Pioneer 335) was planted annually from April to October, with a density of 52,500 plants ha^{-1}. No management regimes were adopted, except for weeding by hand.

Soil sampling and analysis of soil properties

Soil samples from each plot were collected at the flowering stage in early August 2019. In each plot, 10 soil cores were collected from the surface layer (0 − 20 cm) using a Dutch auger (5-cm diameter), and mixed to form a composite sample. After field collection, fresh samples were placed on ice and immediately transported to the laboratory, and then were sieved (2 mm) to remove visible residues. Then, samples were divided into three sections: (1) stored at − 80 °C for measuring the autotrophic bacterial communities, (2) stored at 4 °C for measuring dissolved organic C (DOC), microbial biomass C (MBC), and (3) air-dried for soil chemical properties and RubisCO activity analysis.

Soil pH was measured by a pH meter (Mettler Toledo FE20, Shanghai, China) with water: soil ratio of 2.5: 1 (v/w). SOC was determined by a modified Walkley-Black wet oxidation method (Nelson and Sommers 1983). Soil total N (TN) was determined using the micro-Kjeldahl method (Sparks et al. 1996). Nitrate N (NO_3-N) and ammonium N (NH_4-N) were extracted with 2 M KCl and measured using a continuous flow analyzer (Skalar, Breda, Netherlands). Available phosphorus (AP) was extracted with sodium bicarbonate and measured using the molybdenum-blue method (Olsen 1954). DOC was determined by the method of Jones and Willett (2006). MBC was determined by the $CHCl_3$ fumigation extraction (Vance et al. 1987). Soil water content (SWC) was measured using the oven-dry method (O'Kelly 2004).

RubisCO activity

Soil RubisCO activity was determined by the method described by Yuan et al. (2012b). Briefly, 2 g of freeze-dried soil sample was placed in centrifuge tubes and suspended in protein extractant containing Tris–HCl buffer and dithiothreitol. The soil suspension was disrupted by ultrasonication in ice bath. After centrifuged, the supernatant was amended with solid ammonium sulfate to reach 80% saturation, and then stirred for 30 min and centrifuged at 4℃. The precipitate was dissolved to determine RubisCO activity. The absorbance of reaction mix was measured at 340 nm wavelength using a spectrophotometer (UV − 2450, Shimadzu, Japan). All reactions were carried out in triplicate, and negative controls were set up. The RubisCO activity was expressed as nmol CO_2 g^{-1} soil min^{-1}.

The *cbbL* gene copy number and Illumina sequencing

Total genomic DNA was extracted from soil samples using the EZNA® Soil DNA Kit (Omega Biotek, Norcross, GA, USA) according to manufacturer's protocols. The quality of DNA was determined by 1% agarose gel electrophoresis, and the concentration and purity were detected using a NanoDrop − 2000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). DNA samples were stored at − 80℃ for subsequent analysis.

The copy number of *cbbL* gene was determined by quantitative PCR using the primers K2f (5'-ACCAYC AAGCCSAAGCTSGG-3') and V2r (5'-GCCTTC SAGCTTGCCSACCRC-3') (Tolli and King 2005). The reactions were performed in triplicate 20 μL mixture containing 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase, and 10 ng of template DNA. The PCR parameters were as follows: a pre-denaturation 95 °C for 2 min, followed by 25 cycles at 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 30 s, and a final extension at 72 °C for 5 min. The standard curve was obtained using a 10^2 to 10^8 dilution of plasmid DNA carrying the *cbbL* gene fragment. Melting curve

analysis was performed at the end of the PCR amplification to check the specificity of amplification. The PCR efficiency and correlation coefficients (R^2) for standard curves were 97.0% and 0.99, respectively. The *cbbL* copy number was calculated according to the standard curve.

Purified PCR products were quantified by Qubit3.0 (Life Invitrogen) and mixed equally. The amplicon library was paired-end sequenced (2 × 300) on an Illumina platform. Raw data were extracted, trimmed, and quality screened using the Quantitative Insights Into Microbial Ecology (QIIME, v1.8.0) (Caporaso et al. 2010). Briefly, the low-quality sequencing reads with length < 150, with an average Phred scores < 20, with ambiguous bases in barcodes and with mononucleotide repeats greater than 8 bp were filtered out. The paired reads from the original bacterial DNA fragments were merged using FLASH (version 1.2.7). Chimeric sequences were identified and eliminated through the Uchime algorithm (version 4.2). After chimera detection, sequence analyses were performed with the UPARSE (version 7.1) software package and the operational taxonomic unit (OTU) was clustered at 97% sequence identity by UCLUST (Edgar 2013). The taxonomic assignment was based on the GenBank nucleotide sequence database (http://ncbi.nlm.nih.gov). Alpha-diversity rarefaction analysis was done using the "QIMME alpha-diversity" plugin to check the quality of the achieved sequencing depth. Alpha-diversity (Chao1 richness and Shannon index) of the autotrophic bacterial communities were calculated using MOTHUR software (Schloss et al. 2009), after rarefying all samples to an equal number of 24,138 reads. We have deposited sequencing reads in the Sequence Read Archive at National Center for Biotechnology Information (NCBI) under the accession number PRJNA773586.

Maize yield

All maize plants were manually harvested at maturity. After harvest, the air-dried grain in each plot was weighted to calculate grain yield. The aboveground biomass was determined on a dry-weight basis by oven drying the crop samples at 105 °C for 45 min and subsequently to constant weight at 85 °C (Xie et al. 2020).

Statistical analyses

One-way analysis of variance (ANOVA) was used to determine the differences among N application rate treatments at the 95% confidence level (SPSS 22.0, IBM SPSS, USA). Treatment means was analyzed by Tukey's honest significance test at $p < 0.05$. Pearson's correlation coefficients were used to assess linear relationships among soil properties, the abundance and compositions of soil autotrophic bacterial communities, RubisCO activity, DOC, MBC, and crop yield across N treatments. Principal coordinate analysis (PCoA) was used to evaluate the Bray-Curtis distances of soil autotrophic bacterial community compositions using the 'vegan' package in R software.

To describe the potential co-occurrence patterns, the autotrophic bacterial network was constructed using the Spearman's correlation and Kullback-Leibler dissimilarity (Faust et al. 2012). The OTUs more than five-sixths of soil samples were kept for network construction. A valid co-occurrence was considered a statistically robust correlation between taxa when the correlation coefficient (r) was > 0.6 or < -0.6 and the p value was < 0.05. The co-occurrence network visualization was conducted using Gephi software (Bastian et al. 2009), and the modules were defined as clusters of closely associated nodes (i.e., groups of co-occurring microbes) (Layeghifard et al. 2017).

Random forest tool was used to assess the important predictors of RubisCO activity. Random Forest modeling was conducted using the 'RandomForest' package (Bento et al. 2002), and the 'rfPermute' package was used to determine the model significance and predictor importance (Archer 2016). The significant predictors in the random forest analyses were further chosen to perform structural equation modeling (SEM) analysis. SEM analysis was performed to estimate the direct and indirect contributions of soil properties and the autotrophic bacterial communites to RubisCO activity and maize yield. SEM analysis performed by the robust maximum likelihood evaluation using AMOS 22.0 (SPSS, Chicago, IL, USA). The model fitness was determined according to chi-square test ($p > 0.05$), goodness of fit value, and root mean square error of approximation (Hooper et al. 2008).

Results

Soil properties, yield, and Rubisco activity

One-way analysis of variance showed that the N treatments significant effects on soil properties ($p<0.05$, Table 1). TN and NO_3-N were significantly ($p<0.05$) increased with the increasing rates of N application, while soil pH and SWC exhibited an opposite tread ($p<0.05$). However, no significant difference was found in SOC ($p>0.05$), NH_4-N ($p>0.05$), and AP ($p>0.05$) among the three N treatments (N1, N2, and N3). DOC and MBC were enhanced by the N application (Table 1), with significantly ($p<0.05$) higher values under the N3 treatment than under the N1 and N0 treatments, but no significant difference between N2 and N3 treatments. The N2 and N3 treatments were characterized by significantly ($p<0.05$) higher grain yield and aboveground biomass than the N1 and N0 treatments (Table 1), as well as RubisCO activity ($p<0.05$, Fig. 1a).

Abundance and structure of soil autotrophic bacterial communities

The abundance of autotrophic bacteria indicated by the copy number of *cbbL* gene ranged from 0.82×10^6 to 2.78×10^6 copies g^{-1} soil. The significant ($p<0.05$) differences were observed among treatments, with the highest abundance of *cbbL* gene under the N3 treatment (Fig. 1b). A total of 289, 656 sequences of soil autotrophic bacterial communities were obtained using Illumina sequencing after quality control. The diversity of autotrophic bacteria indicated by Chao 1 richness was significantly higher under the N0 and N1 treatments than under the N2 treatment, with intermediary value under the N3 treatment ($p<0.05$, Fig. 1c). However, there was no significant difference in Shannon index among the four treatments ($p=0.10$, Fig. 1d).

Across all samples, Alphaproteobacteria (32.4%), Betaproteobacteria (10.7%), and Actinobacteria (10.4%) dominated the autotrophic bacterial communities (Fig. 2a). The dominant communities were mainly affiliated with facultative autotrophic bacterial genera *Xanthobacter* (10.8%), *Bradyrhizobium* (10.1%), *Aminobacter* (5.2%), *Nitrosospira* (6.1%) and, *Mycobacterium* (2.9%), followed by the rare genera *Nocardia* (1.9%), *Oscillochloris* (1.8%), *Sphingomonas* (1.5%), and *Saccharomonospora* (1.3%), (Fig. 2b). The relative abundance of *Xanthobacter* under the N3 treatment was significantly ($p<0.05$) higher than those under the N0, N1, and N2 treatments, while *Nocardia* and *Saccharomonospora* under the N1, N2, and N3 treatments were significantly ($p<0.05$) lower than that under the N0 treatment. Principal coordinate analysis indicated that the composition of autotrophic bacterial communities under the N2 and N3

Table 1 Soil properties and maize yield under four N treatments

	N0	N1	N2	N3
pH	8.56 ± 0.02a	8.48 ± 0.06ab	8.40 ± 0.01bc	8.36 ± 0.01c
TN (g kg^{-1})	0.86 ± 0.01c	0.92 ± 0.01b	0.97 ± 0.20ab	1.01 ± 0.02a
NO_3-N (mg kg^{-1})	18.15 ± 1.46c	21.03 ± 1.01bc	23.49 ± 1.00ab	27.29 ± 1.86a
NH_4-N (mg kg^{-1})	16.82 ± 0.57a	18.96 ± 0.09a	20.31 ± 1.45a	20.96 ± 3.28a
AP (mg kg^{-1})	16.56 ± 0.60a	13.86 ± 1.76a	15.55 ± 1.02a	13.79 ± 0.94a
SWC (%)	21.77 ± 0.61a	20.66 ± 0.20ab	19.58 ± 0.17bc	19.48 ± 0.06c
SOC (g kg^{-1})	7.55 ± 0.23b	8.47 ± 0.10a	8.64 ± 0.08a	8.75 ± 0.05a
DOC (mg kg^{-1})	125.6 ± 2.6c	132.8 ± 1.4bc	142.7 ± 5.6ab	152.2 ± 7.4a
MBC (mg kg^{-1})	110.9 ± 13.9c	138.6 ± 6.9b	173.3 ± 18.3a	194.0 ± 18.3a
Grain yield (kg ha^{-1})	4156 ± 289c	6850 ± 927b	11,859 ± 785a	11,517 ± 100a
Biomass (kg ha^{-1})	12,336 ± 703c	19,890 ± 2890b	28,948 ± 2807a	27,596 ± 1960a

Within a row, means (n = 3) ± standard error followed by different letters are significant at $p<0.05$. TN, total N; NO_3-N, nitrate N; NH_4-N, ammonium N; AP, available phosphorus; SWC, soil water content; SOC, soil organic C; DOC, soil dissolved organic C; MBC, microbial biomass C. N0, N1, N2, and N3 represent N application at 0 kg ha^{-1}, 100 kg ha^{-1}, 200 kg ha^{-1}, and 300 kg ha^{-1}, respectively

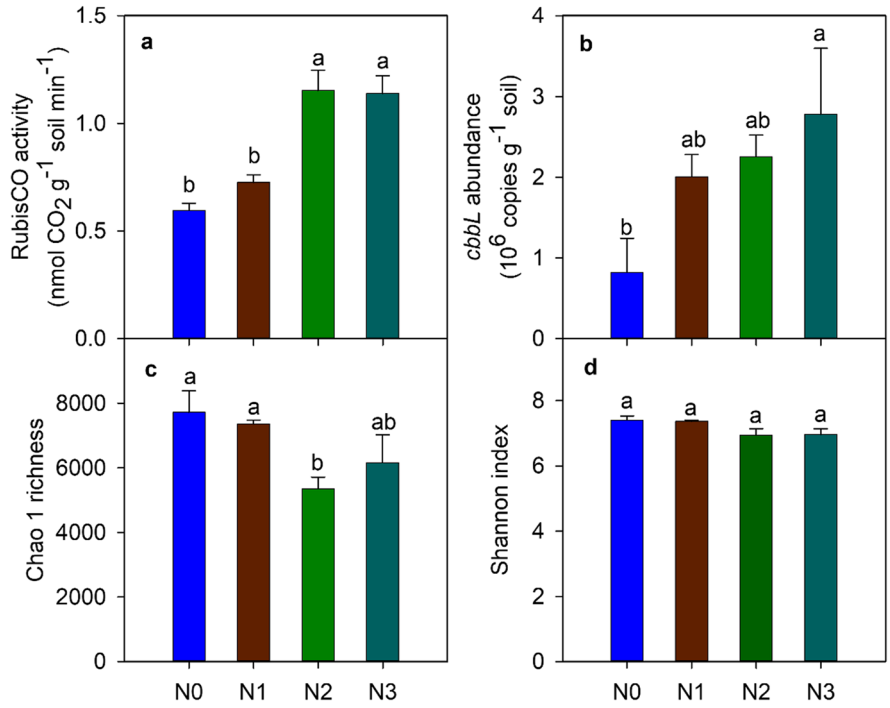


Fig. 1 Soil RubisCO activity (**a**) and *cbbL* gene copy numbers (**b**), and alpha-diversity (**c** and **d**) autotrophic bacteria under different N application rate treatments. Different letters indicate the significant difference among treatments at $p < 0.05$. Bars represent standard errors (n = 3). N0, N1, N2, and N3 represent N application at 0 kg ha^{-1}, 100 kg ha^{-1}, 200 kg ha^{-1}, and 300 kg ha^{-1}, respectively

treatments exhibited a significant ($p < 0.001$) separation from that under the N1 and N0 treatments (Fig. S2).

The abundance and community compositions of autotrophic bacteria were positively correlated with NO_3-N ($r = 0.57$, $p < 0.05$ and $r = 0.79$, $p < 0.01$), but negatively correlated with pH ($r = -0.57$, $p < 0.05$ and $r = -0.75$, $p < 0.01$) and SWC ($r = -0.62$, $p < 0.05$ and $r = -0.83$, $p < 0.001$) (Fig. 3). The abundance and community compositions of autotrophic bacteria had positive correlations with RubisCO activity ($r = 0.58$, $p < 0.05$ and $r = 0.91$, $p < 0.001$), SOC ($r = 0.63$, $p < 0.05$ and $r = 0.75$, $p < 0.01$), DOC ($r = 0.90$, $p < 0.001$ and $r = 0.73$, $p < 0.01$), as well as maize yield ($r = 0.65$, $p < 0.05$ and $r = 0.94$, $p < 0.001$), and aboveground biomass ($r = 0.61$, $p < 0.05$ and $r = 0.91$, $p < 0.001$) (Fig. 3). In contrast, the autotrophic bacterial diversity showed negative correlations with TN ($r = -0.74$, $p < 0.01$), NO_3-N ($r = -0.70$, $p < 0.05$), RubisCO activity ($r = -0.57$, $p < 0.05$), DOC ($r = -0.69$, $p < 0.05$), maize yield ($r = -0.71$, $p < 0.05$), and aboveground biomass ($r = -0.73$, $p < 0.01$).

The autotrophic bacterial co-occurrence networks

Co-occurrence networks were constructed to examine the different co-occurrence patterns of the soil autotrophic bacterial communities under the four treatments (Fig. 4). In total, there were 367 nodes, 1956 links, and four distinct modules (modules I, II, III, and VI) in the autotrophic bacterial network. In the autotrophic bacterial network, the number of positive correlations (1953 edges) were greater than that of the negative correlations (3 edges). The modules I, II, III, and VI in the bacterial networks consisted of 117, 72, 99, and 79 nodes, respectively. At the phylum level, the relative abundance of Alphaproteobacteria was significantly ($p < 0.05$) higher in modules II and VI than in modules I and III, while those of Betaproteobacteria, Actinobacteria, and Chloroflexi followed the opposite trend (Fig. 5a). At the genus level, modules I and II showed the significantly ($p < 0.05$) greater abundances of *Aminobacter* and *Bradyrhizobium*, but lower abundances of *Mycobacterium*, *Nitrosospira*, and *Saccharomonospora* than module III. In contrast, *Xanthobacter* was significantly greater in module VI than in modules I, II, and III (Fig. 5b).

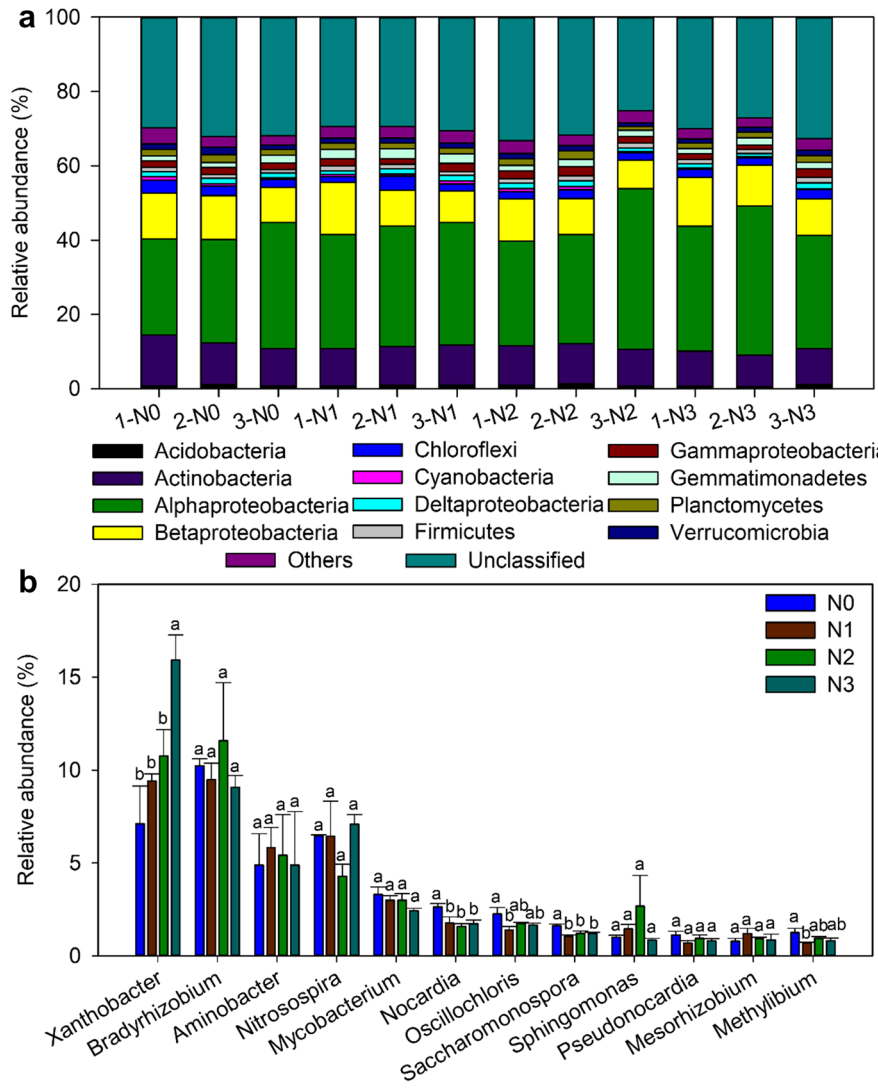


Fig. 2 Relative abundance of the autotrophic bacterial phyla under different N application rate treatments (**a**). The numbers before the treatment name indicate the sampling replications, for example, 1-N0, 2-N0, and 3-N0 means the sampling was taken from replicate 1, 2, and 3 of the field plots, respectively. (**b**) Relative abundance of the autotrophic bacterial genera under different N application rate treatments. Different letters indicate the significant difference among treatments at $p < 0.05$. Bars represent standard errors (n = 3). N0, N1, N2, and N3 represent N application at 0 kg ha^{-1}, 100 kg ha^{-1}, 200 kg ha^{-1}, and 300 kg ha^{-1}, respectively

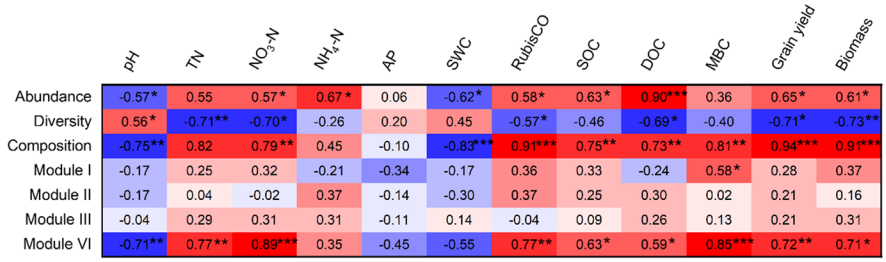


Fig. 3 Correlation coefficients between soil autrotrophic bacterial communities, soil properties, RubisCO activity, SOC storage, and yields. NO_3-N, nitrate N; NH_4-N, ammonium N; AP, available phosphorus; SWC, soil water content; RubisCO, RubisCO activity; SOC storage including soil oraganic C (SOC), microbial biomass C (MBC), and dissolved organic C (DOC). The autotrophic bacterial commmunities are represented by abundance of *cbbL* gene, diversity (Shannon index), composition (first principal coordinates, PCoA1), and and the eigengenes of four modules (modules I, II, III, and VI) in trophic co-occurrence network. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

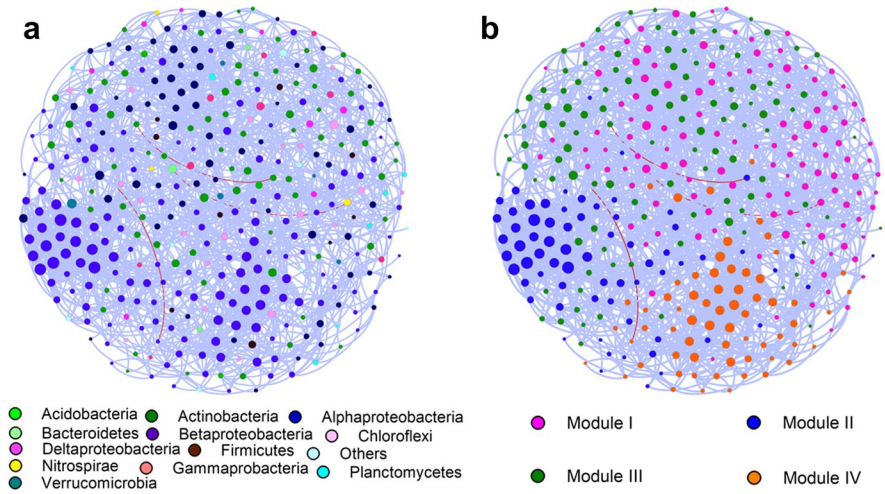


Fig. 4 Co-occurrence network of soil autotrophic bacterial communities under four treatments. The network is colored by phyla (**a**) and modules (**b**), respectively. Modules I–IV represent four clusters with closely interconnected nodes. Size of each node is proportional to the number of connections (degree), and the thickness of each connection between two nodes (edge) is proportional to the value of correlation coefficients. Blue edges indicate positive connections, red edges negative connections

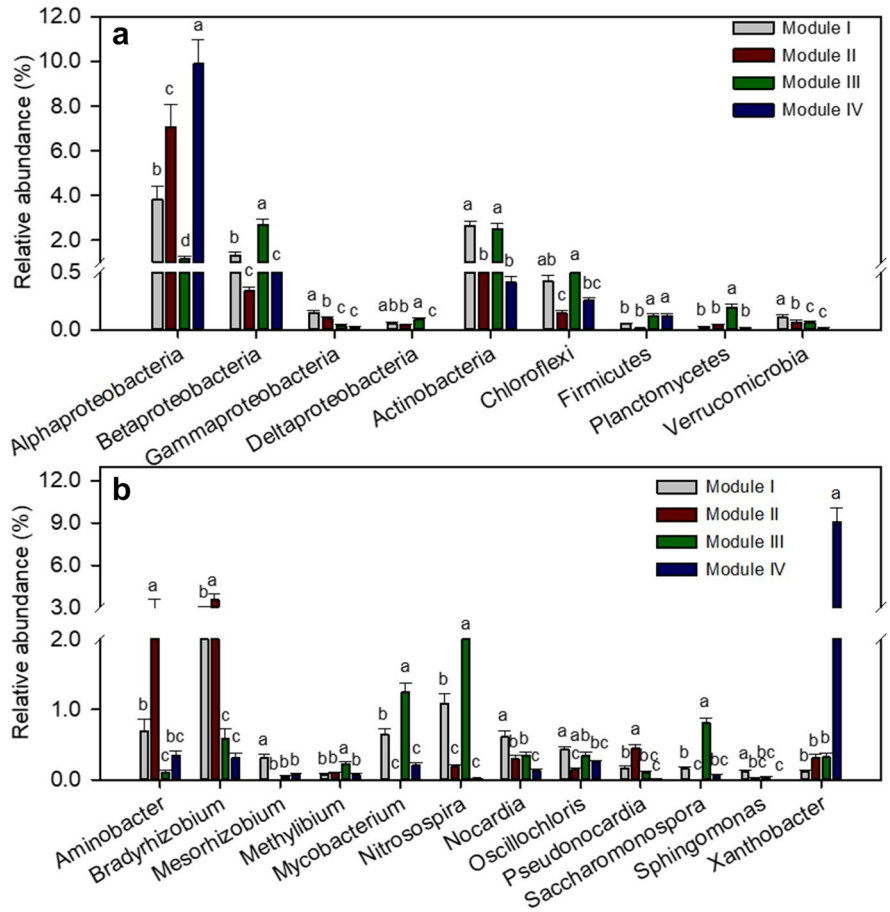
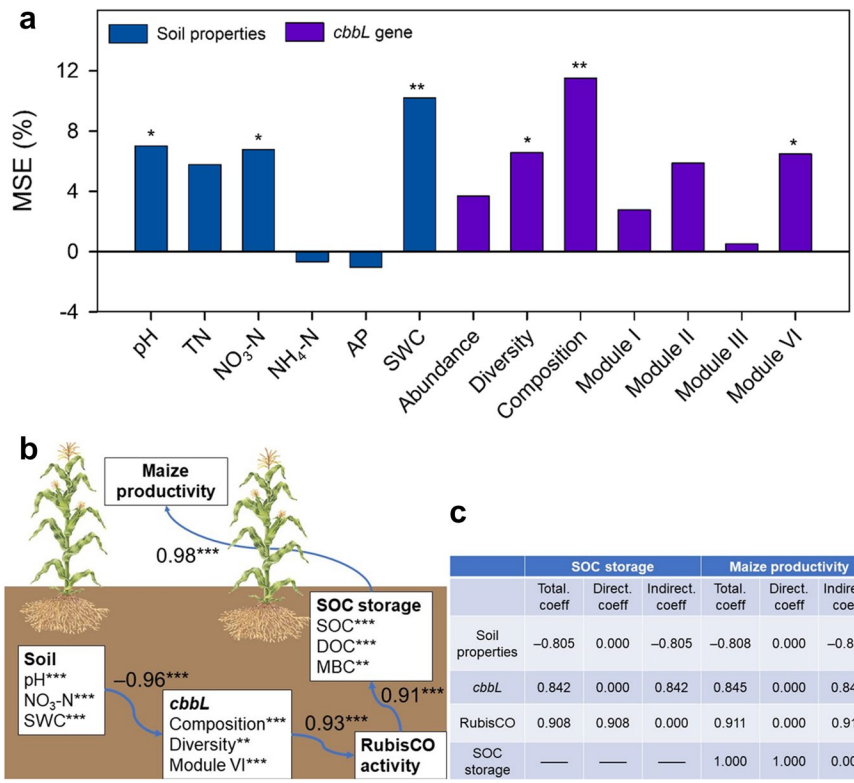


Fig. 5 Relative abundance of different dominant modules in soil autotrophic bacterial networks at phyla (**a**) and genera (**b**)-level. Different small letters indicate the significant difference among modules at $p < 0.05$. Bars represent standard errors (n = 12)

Module VI was positively correlated with TN ($r=0.77$, $p<0.01$) and NO_3-N ($r=0.89$, $p<0.001$), but negatively correlated with pH ($r=-0.71$, $p<0.01$) (Fig. 3). Furthermore, module VI had positive correlations with RubisCO activity ($r=0.77$, $p<0.01$), SOC ($r=0.63$, $p<0.05$), DOC ($r=0.59$, $p<0.05$), MBC ($r=0.85$, $p<0.001$), grain yield ($r=0.72$, $p<0.01$), and aboveground biomass ($r=0.71$, $p<0.05$) (Fig. 3).

Soil properties and autotrophic bacterial communities affected RubisCO activity and maize yield

Random forest modeling revealed that pH (7.0%, $p<0.05$), NO_3-N (6.8%, $p<0.05$), and SWC (10.2%, $p<0.01$) were the primary predictors among soil properties for RubisCO activity (Fig. 6a). As for the autotrophic bacteria, RubisCO activity was significantly affected by the compositions (11.5%, $p<0.01$), diversity (6.5%, $p<0.05$), and module VI in the network (6.5%, $p<0.05$) of the autotrophic



	SOC storage			Maize productivity		
	Total. coeff	Direct. coeff	Indirect. coeff	Total. coeff	Direct. coeff	Indirect. coeff
Soil properties	–0.805	0.000	–0.805	–0.808	0.000	–0.808
cbbL	0.842	0.000	0.842	0.845	0.000	0.845
RubisCO	0.908	0.908	0.000	0.911	0.000	0.911
SOC storage	——	——	——	1.000	1.000	0.000

Fig. 6 Mean contribution (% of increased mean square error, MSE) of soil properties and soil autotropic bacterial communities (*cbbL*) to RubisCO activity based on random forest modeling (**a**). Random forest modeling was performed based on 12 samples (4 fertilization treatments × 3 replicates). Soil properties include pH, total nitrogen (TN), nitrate N (NO_3-N), ammonia N (NH_4-N), available phosphorus (AP), and soil water content (SWC). The autotrophic bacterial communities include abundance of *cbbL* gene, diversity (Shannon index), composition (first principal coordinates, PCoA1), and four module eigengenes in trophic co-occurrence network. (**b**) the impacts of soil properties and soil autotrophic bacterial communities on RubisCO activity, SOC storage, and maize productivity (grain yield) as estimated using structural equation modeling (SEM) analysis. Based on random forest analyses, the significant predictors were chosen to perform the SEM analysis. The latent (soil properties and the autotrophic bacterial communities) inside the boxes were used to integrate the effects of multiple conceptually related observed variables into a single-composite effect. (**c**) the total, direct, and indirect effects of soil properties, soil autotrophic bacterial communities (*cbbL*), RubisCO activity, and SOC storage on SOC storage and maize productivity. Soil properties are represented by pH, nitrate N (NO_3–N), and soil water content (SWC). Soil autotrophic bacterial communities (*cbbL*) are represented by the composition [first principal coordinates (PCoA1)], diversity (Shannon index), and module VI of soil autotrophic bacterial networks. SOC storage is represented by soil organic C (SOC), microbial biomass C (MBC), and dissolved organic C (DOC). *** $p<0.001$; ** $p<0.01$; * $p<0.05$

bacterial communities. Structural equation modeling (SEM) further suggested that soil properties were significantly ($p < 0.01$) correlated with the autotrophic bacterial communities (Fig. 6b). Soil properties and the autotrophic bacterial communities could indirectly influence SOC storage and maize yield (Fig. 6c). Importantly, soil autotrophic bacterial communities might significantly ($p < 0.001$) affect RubisCO activity through compositions, diversity, and module VI. Therefore, they positively impacted SOC storage, which is essential for maintaining soil fertility for maize yield.

Discussion

N application affected soil autotrophic bacterial communities and RubisCO activity

Our results showed that N fertilizer application led to great changes in soil properties, and consequently strongly impacted the abundance, diversity, and composition of soil autotrophic bacterial communities. The abundance of *cbbL* gene was significantly increased with increasing application rate of N fertilization, with the highest value under the N3 treatment. Increasing *cbbL*-containing bacterial abundance has been found to be positively correlated with microbial CO_2 fixation rate (Yuan et al. 2012b; Wu et al. 2015). Observations of the large abundance were probably derived from the high level of TN and available N (NO_3–N and NH_4–N), and pH closer to neutral under the N3 treatments. Soil pH has been evidenced as the main factor influencing the microbial diversity and community structure (Jiang et al. 2016; Ramírez et al. 2020). Soil pH close to neutral is significantly related to high nutrient availability and increased microbial diversity (Rousk et al. 2010; Liu et al. 2021). The nutrient availability may provide spatially adaptive microhabitats for the autotrophic bacterial communities, and thus favor the growth and colonization of facultative autotrophs. We found that the N application significantly reduced Chao1 richness, suggesting an overall decline of soil autotrophic bacterial diversity. Appropriate and balanced fertilization increase soil microbial diversity, while excessive N application leads to a decrease in soil microbial diversity, mostly due to the decreasing pH under long-term N fertilization (Shen et al. 2010; Wang et al. 2018).

In the present study, the impact of N application on soil autotrophic bacterial community compositions were significantly associated with soil properties. The majority of the autotrophic bacterial communities belonged to the facultative autotrophic bacteria. These populations exhibit diverse eco-physiological traits and advantageous ecological strategies for C fixation and the degradation of various C-containing organic compounds (Yuan et al. 2012b; Guo et al. 2015; Ge et al. 2016; Liao et al. 2020). We further discovered that the co-occurrence network of autotrophic bacteria contained distinct microbial modules consist of highly interconnected taxa. The intimate connections among species in the microbial network may represent their niche sharing (Berry and Widder 2014; Yuan et al. 2021b). The modules have been reported as ecological niche overlap, habitat heterogeneity, and phylogenetic relatedness (Freilich et al. 2010), which have different functions in nutrients exchange and resource availability in agricultural ecosystems (Jiang et al. 2017; Li et al. 2021). We should be cautious about the bacterial relationships from co-occurrence network because statistical correlations do not necessarily represent causal relationships.

Soil RubisCO has been used as a key indicator of autotrophic microbial assimilation of atmospheric CO_2 (Wu et al. 2014), which has significant positive roles in soil C-fixation activity based on a ^{14}C-label microcosm experiment (Yuan et al. 2012a). Although a large number of field experiments have been conducted to examine the effect of fertilization on soil RubisCO activity, how N fertilizer affects soil RubisCO activity remains still debated (Liao et al. 2020; Yuan et al. 2012b). Soil pH has often been reported to show considerably distinct effects on soil RubisCO activity (Guo et al. 2015; Zhou et al. 2019). Our results indicated that N fertilizer was beneficial for increasing soil RubisCO activity in a weak alkaline soil, which is opposite to the finding of Liao et al. (2020) that N fertilization inhibits Rubisco activity in acidic soil (pH < 7).

Soil autotrophic bacterial communities mediated SOC storage

Several research have shown that soil autotrophic bacterial communities contribute substantially to C fixation and SOC pool dynamics in farmland systems (Yuan et al. 2012a; Ge et al. 2016). A previous

study has reported that the microbial C-fixing rate ranges from 0.84 to 5.57 Mg C km^{-2} per year in the Qiaozi watershed of the Chinese Loess Plateau (Xiao et al. 2018b). We found that the abundance and compositions of the autotrophic bacterial communities were positively correlated with RubisCO activity. The close relationship between RubisCO activity, ^{14} C-SOC, and the abundance of *cbbL* gene confirms that soil C fixation is carried out by the soil autotrophic bacterial communities by regulating RubisCO activity (Yuan et al. 2012a). Soil microbial diversity is of ecological importance to predict multiple ecosystem functioning, including nutrient cycling and climate regulation (Delgado-Baquerizo et al. 2016; Jiao et al. 2021). However, few studies have explicitly addressed how and to what extent soil autotrophic bacterial diversity drives soil C fixation. Our study showed that the diversity of the autotrophic bacteria negatively correlated with DOC, MBC, and maize yield. High diversity induced negative priming of SOC through the complicate relationship among taxa in microbial networks (Xiao et al. 2018a; Chen et al. 2019). Highly similar species share similar microhabitats suppress C metabolism as species diversity increases (Maynard et al. 2017). We confirmed that the reduced autotrophic bacterial diversity enhanced RubisCO activity and CO_2 fixation rate of bacterial populations, and positive response of bacterial CO_2 fixation to the N fertilization can increase SOC accumulation, which is a benefit for soil fertility, indicated by a higher maize production. The soil autotrophic bacterial communities were dominated by facultative autotrophic bacteria, including *Xanthobacter*, *Bradyrhizobium*, *Aminobacter*, and *Nitrosospira*. In fact, these facultative autotrophs exhibit metabolic flexibility with both heterotrophic and autotrophic metabolic pathways, allowing them to grow on alternative C and energy sources (Esparza et al. 2010; Xiao et al. 2019). Additionally, the genus *Xanthobacter* is the main implementer of fixing CO_2 mainly via the ribulose-biphosphate pathway (Wiegel 2006). Notably, the genus *Xanthobacter* was the dominant taxa in module IV of co-occurrence network, and module IV had positive correlations with SOC storage, which confirmed the potentials of soil autotrophic bacterial communities for C fixation. Our results highlight that soil autotrophic bacteria have significant potentials for C fixation and contribute to C pool and crop productivity.

Conclusions

The present study indicated N strongly impacted the abundance, diversity, composition, and co-occurrence network of soil autotrophic bacterial communities via changing pH, NO_3-N, and SWC. We provided evidence that the abundance, diversity, and network of soil autotrophic bacterial communities contributed to RubisCO activity, SOC storage, and maize productivity. Taken together, understanding the biological mechanisms of soil autotrophic bacteria mediating C fixation may provide crucial implications for enabling SOC sequestration that is a benefit for maize productivity. Future research on microcosm and stable isotope-based could help verify the casual relationships between soil autotrophic bacterial communities and C fixation activity.

Acknowledgements This work was supported by the Education science and technology innovation project of Gansu Province (GSSYLXM – 02), the Fostering Foundation for the Excellent Ph.D. Dissertation of Gansu Agricultural University (YB2020002), the National Natural Science Foundation of China (31761143004, 41922048), the Innovation Star Project for Excellent Graduate Student of Gansu Province Educational Department (2021CXZX-369), the Department of Science and Technology of Gansu Province (GSPT – 2018 – 56), and the Young Instructor Fund Project of Gansu Agricultural University (GAU-QDFC-2020-03).

Author contributions Ling Li and Yuji Jiang conceived the topic. Jinbin Wang, Junhong Xie, Zhuzhu Luo, and Renzhi Zhang performed the experiments. Jinbin Wang analyzed all statistical data. Jinbin Wang and Yuji Jiang wrote the manuscript. All authors have read and approved the manuscript.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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