Revealing the Tomato Endophyte Bacteria Communities Under Long-term Organic and Conventional Agricultural Practice System

Zeyu Zhang

china agricultrual university

Yabin Zhan

College of Resources and Environmental Science, China Agricultural University, Beijing 100193, China

Zengqiang Zhang

College of Resources and Environmental Science, Northwest A&F University, Yanglin 712021, China

Youzhou Liu

Institute of Plant Protection, Jiangsu Academy of Agricultural Sciences, Nanjing 210000, China

Ting Xu

College of Resources and Environmental Science, China Agricultural University, Beijing 100193, China

Yuquan Wei

College of Resources and Environmental Science, China Agricultural University, Beijing 100193, China

Ji Li (✉ liji@cau.edu.cn)

College of Resources and Environmental Science, China Agricultural University, Beijing 100193, China

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Abstract

Purpose: Microorganisms associated with the plant can contribute to plant health. Discrepancy both soil microbial structure and physicochemical properties observed in the organic and conventional agricultural systems. However, very little is known about the diversity of endophytic bacterial communities in plants grown in separate manipulation systems. The goal of this work was to get a broader overview of the diversity and dynamics of the tomato endophytic bacteria in the different agricultural practice systems.

Methods: The structure of tomato endophyte bacterial communities under different growing stage (seeding stage, flowering stage, fruiting stage and harvesting stage), agricultural manipulation practices (organic and conventional systems) and organ-type (root or stem) were explored by using 16S rRNA gene profiling in this study.

Results: A total of 2,014,992 16S rRNA gene sequences were obtained. These sequences revealed large-scale functional taxonomy units (OTUs). That is, there are 648 different OTUs in libraries, and 96 OTUs are common. Tomato endophyte bacteria consisted mainly of four phylum, of which Proteobacteria was the most represented, followed by Firmicutes, Bacteroides, Actinobacteria, Gamma proteobacteria, the most abundant class are proteobacteria, bacteriobacteria, and so on. Proteobacteria are low. Enterobacteriaceae, Veella, Bacillus, Mesorhizobium and Chrysobacterium were shared by all plant development stage. Rich endophytic bacterial diversity was observed at the seedling stage (T1), and endophytic bacterial diversity at the flowering stage (T2) and fruiting stage (T4) was low. Significant difference in endophytic bacterial communities emerged from roots and different host biographical stages, and tomato exerts greater influence on endophyte bacteria compared to organ type (main) agricultural manipulation methods.

Conclusions: Tomato endophyte microbiota have a distinct structure in different plant development stage. *Bacillus*.spp were enriched seeding stage (T1) and decreased in the fruiting stage while *Mesorhizobium*.spp increased during in the fruiting stage (T4). Tomato have distinct endosphere microbiota by comparing beta diversity of microbiota in all crop season, compared with the manipulation resume and organ niche. And a strong correlation was observed between the structure of the microbiota in the whole dataset and soil chemistry which indicated that the soil type and treatment affected the endosphere microbiota of tomato. Organ niche exert more influence on the tomato microbiota compared with agricultural treatments between organic-farming and conventional farming.

Introduction

Tomato (*Solanum lycopersicum* L.) are an important economic crop grown worldwide that are of commercial value and ecological importance. Evidence is increasing that microorganisms associated with crop play an important role in plant health (Zhao et al. 2016). Plant microorganisms, often recalled plant second genome, are essential for plant health (Rui et al. 2019), of which related to the plant nutrition and resistance to biological stress (Cao et al. 2004). Therefore, it is important to have a good

understanding of the microbial communities. Bacteria can also live and thrive inside their host plants, which are called endophytes. Endophytes have been isolated from different parts of plants that are above and below ground including roots, stems, leaves, flowers, fruits, tubers and seeds (Manzotti et al. 2020). Bacterial endophytes normally completed their life cycle within host plants enhancing the plants to any tolerance to biotic and abiotic stresses (Kahremani et al. 2019). In addition, endophytic microorganisms can provide protection against fungal diseases, which can directly promote plant growth via phytohormone production, nutrient solubilization, and nitrogen fixation and metabolism (Vector J et al. 2011).

Till now, little information is available about the bacterial community structure of tomato cultivated in a greenhouse environment, which has been widely used in tomato production. Exploring the structure of microbiota can help clarify their function and potentially improve performance. (Constantine et al. 2019).

Endophyte microbiota can be affected by a variety of factors such as physical and chemical properties and good farming practices such as organic farming and microbial vaccination. E.g., and plant yields generally excel in organic farming suitable for plant growth (Dong et al. 2019). Good agricultural practices, e.g., agricultural microbial inoculants, for example, generally improve the yield of crop during organic farming (Hon et al. 2017).

A long-term organic farming experiment was carried out in 2002 at the Quzhou Experimental Station in Hebei Province, China. All two farming systems were under the same agricultural practice including crop rotation, irrigation and plowing, but they differed in fertilization and plant protection management. Differences were found in both the microbial structure and the physicochemical properties (Han et al. 2017). However, little is known about the endophytic bacterial communities in plants grown under separate greenhouse. The structure of endophyte bacterial communities under different plant development stage (seeding stage, flowering stage, fruiting stage and harvesting stage), organic and conventional agricultural practices and organ niche (root or stem) were explored in this study using 16S rRNA gene amplicon sequencing.

This study provides comprehensive insight into the bacterial communities associated with tomato cultivated in a greenhouse agro-ecosystem and provides useful information for the control of potential pathogens and promoting production in tomato cultivation.

Materials And Methods

Growth Conditions and Sample Collection

The field experiment was conducted in Quzhou county, Hebei province (36°52'N, 115°01'E), and the long-term greenhouse experiment was set up in March 2002. The experiment consists of organic (ORG), low-input (LOW), and conventional (CON) systems. Each system had three semi-round arch greenhouses (52 m in length and 7 m in width for each greenhouse). Crop varieties, irrigation, and tillage schemes are the same in all three systems in the same growing season.

Tomato samples (*S. lycopersicum* cultivar “Zhongza 302”) were collected from the research greenhouse located in the organic and conventional greenhouse, and four plant developmental stages, including seedling the stage, flowering stage, fruiting stage, and harvesting stage were chosen during the growth period from March 2019 to August 2019. Thus 80 plant samples were sampled in total. Surface sterilization were performed in previously described (Gu et al. 2020), till no bacterial growth was detected after plating the roots on R₂A agar at 30°C for 7 days (Mcperson et al. 2018).

PCR Amplification and MiSeq High-Throughput Sequencing

PCR optimization and Illumina-Hiseq250 pyrotechnical were performed by the Amplicon Seq Service of the Biomak Biotechnology (China). Briefly, DNA aliquots (10 ng) were PCR-amplified at 94 for 30 s and then 30 cycles of 94 for 20 s, 45 for 20 s, and 65 for 60 s; with a final extension at 72 for 5 min. V7-V9 hypervariable regions of the bacterial 16S rRNA gene were amplified with the primers 799 F and 1193 R containing the sequencing adapters and sample-specific barcode (Illumina-Hiseq250 Sciences). The applicants were purified and quantified fluorometrically with the Min Elute kit (Qiagen, Germany).

Sequence Analysis

The raw 16S rRNA gene sequencing reads were demultiplexed, quality-filtered by fastq version 0.20.0 and merged by FLASH version 1.2.7 with the following criteria: (i) the 300 bp reads were truncated at any site receiving an average quality score of < 20 over a 50 bp sliding window, and the truncated reads shorter than 50 bp were discarded, reads containing ambiguous characters were also discarded; (ii) only overlapping sequences longer than 10 bp were assembled according to their overlapped sequence. The maximum mismatch ratio of overlap region is 0.2. Reads that could not be assembled were discarded; (iii) Samples were distinguished according to the barcode and primers, and the sequence direction was adjusted, exact barcode matching, nucleotide mis match in primer matching (Chen et al. 2020).

Nucleotide Sequence Accession Numbers

The datasets supporting the conclusions of this article are available in the National Center for Biotechnology Information (NCBI) repository (<https://www.ncbi.nlm.nih.gov/bioproject/PRJNA316593/>), under accession numbers SRR6214539. Data can be obtained from the BioSample database (<https://www.ncbi.nlm.nih.gov/biosample/>).

Results

Analysis of sequencing data

A total of 2,014,992 high-quality, non-plastid sequences were requested. The number of sequences per sample varied from 30,702 to 267,257 (Table. S1), and the rarefaction curves shown in Fig.1, which suggested that these libraries detected a large majority of the endophytic bacterial diversity in the samples used in our study. Core microbiome analysis showed that total of 648 OTUs were consulted on 80 samples for the bacterial library, with 96 OTUs in common after filtering process (Fig.2).

Taxonomic distributions of tomato endophytic bacteria

The taxonomic summary revealed that the tomato endophyte bacteria mainly comprised four phyla (Fig. 3A), among which Proteobacteria was the most represented ($40.63 \pm 2.68\%$), followed by Firmicutes ($21.76 \pm 1.66\%$), Actinobacteria ($20.3 \pm 3.62\%$) and Bacteroidetes ($8.7 \pm 4.45\%$). A total of 253 different genus were identified across all samples, in addition, the relative abundance of the top 10 most abundant genus was shown in Fig. 3B. The core members of genus within the tomato samples were *Weissella*, *Bacillus*, *Mesorhizobium* and *Chryseobacterium*.spp. A heatmap was constructed to illustrate the relative abundance dynamics of the 10 most abundant genus in the whole crop season (Figure3C,3D). The abundance of *sphingobacterium*.spp and *Streptomyces*.spp gradually increased in the tomato roots under the organic practice greenhouse, while the *Bacillus*.spp gradually decreased. And the similar results in the tomato stem endophyte showed that the abundance of *Arthrobacter*.spp, *Rhizobium*.spp gradually increased, while the *Bacillus*.spp gradually decreased at the late crop season. The abundance of *Bacillus*.spp and *Acinetobacter*.spp gradually decreased in tomato roots, and the abundance of *sphingobacterium*.spp and *Streptomyces*.spp gradually increased in the conventional agricultural greenhouse. And the abundance of *Bacillus*.spp gradually decreased in stem endophyte, and the abundance of *Arthrobacter*.spp and *Rhizobium*.spp gradually increased.

Endosphere communities are diverse among tomato organ niche

The alpha diversity (Shannon index) of microbiota had no significant difference in different plant development stage (Fig. 4A). However, Shannon diversity index of microbiota from the endosphere-root sample were more diverse than those from the endosphere-stem sample either organic or conventional agricultural practice ($P < 0.001$, Fig. 4B).

The beta diversity and PCoA analyses using Bray–Curtis distance matrices showed that bacterial microbiota of different organ niche in four plant growth periods datasets were separated in the first two coordinate axes (Fig. 5A, permutations analysis of variance, Bray–Curtis distance, $R^2 = 0.084$, $P = 0.003$). Tomato endosphere microbiota were distinguished from the seeding, flowering, fruiting and harvesting stage. Principal coordinate analysis (PCoA) of Bray-Curtis distance showed that endosphere microbiota in four development stage separated clusters in the first two coordinate axes (Fig. 5B, permutations analysis of variance, Bray–Curtis distance, $R^2 = 0.173$, $P = 0.001$), and all of the profiles indicated that endosphere microbiota changed with the plant development time.

Tomato endosphere microbiota in different organ niche and agricultural practices treatments were also distinct. Specifically, the seeding stage (T1, Fig. 5C-E), flowering stage (T2, Fig. 5F-H), fruiting stage (T3, Fig. 5I-K) and harvesting stage (T4, Fig. 5L-N) datasets selected were used to analysis the organ niche and agricultural practice treatment factor. Organic system root endophyte (ORGR), conventional system root

endophyte (CONR), organic system stem endophyte (ORGS), conventional system stem endophyte (CONS) datasets from each plant development stage were used to analysis the agricultural practice treatment factor. Seeding stage (TI) datasets selected from the whole dataset were used to analysis the organ niche factor, and root (R) and stem (S) datasets were used to analysis the agricultural practices system factor at seeding stage (Figs.5C-N). The beta diversity and PCoA analyse using Bray–Curtis distance showed that bacterial microbiota of different organ niche in four sampling time datasets were separated in the first two coordinate axes (permutations analysis of variance $R^2 = 0.283$, $P=0.001$), and similar trend occurred in the flowering stage, fruiting stage and harvesting stage.(Figs. 5F,5I, 5L).However, agricultural practices treatment factors had no cluster in different datasets and rarely separated in the first two coordinate axes (Figs.5D,5E, 5G,5H, 5J,5K,5M,5N).

Discussion

During the long-term organic farming experiment from Quzhou county in 2002, three agricultural practice were carried out. Here, we explore the endophyte constitution under two agricultural practice systems. In general, the diverse from rhizosphere to rhizosphere to phylloxera to endosphere is minimal (Lee et al. 2018), so low abundance and diversity in root and stem endophyte bacterial are reasonable in this study. No significance was found in alpha diversity over different plant development time (Fig. 3A). The endophyte bacteria come from the environmental soil, air, air or water (Doju et al. 2018), and endophyte bacteria from the roots can migrate or be transported to the upper parts of plants over time (Lamo et al. 2018) ,of which explain the greater richness in the roots compared to the stems (Zhuang et al. 2020). Similar results were reported for other plants such as Arabidopsis, rice and agave species (Paul Schulz et al. 2018).

It is widely accepted that assembly of endosphere microbiome in plant is driven by many aspects, including climate environment, soil source, host developmental stage, cultivation practice, and root architecture (Ye et al. 2018), and our research showed that organ niche varieties as well as different plant development stage recruited distinct endophyte microbiota (Figs.5B,5C,5F,5I,5L), suggesting that the niche had an significant impact on endophyte microbiota establishment, while agricultural practice exerted limited influence on the constitution endophytes bacteria under greenhouse condition. As the plant organ-type (niche) explained 29.0% of the differential abundance in endophytic microbiota, and it will be essential to provide a clue for screening the beneficial microbiota involved in promoting growth and resisting the diseases (Valenzuela et al. 2018).

Tomato endosphere microbiota mainly composed Proteobacteria, Bacteroidetes, and Acidobacteria. Moreover, the identified core OTUs mostly belonged to the most abundant groups, including Acidobacteria, Sphingobacteriales, Xanthomonadales, Nitrospirales, and this finding was consistent with the previous reports in other plant species, including Arabidopsis, soybean, rice and some of its relatives (Constantin et al. 2019), and the genus *Acinetobacter*, *Enterobacter*, *Pseudomonas* and *Pantoea* were abundantly present in these samples, albeit in different amounts in the vegetative tissues (roots, stems and leaves) (Bulgarelli et al. 2012).

Coordination between the host plant and the microbiota is critical for plant growth in natural environments. We found that roots recruited a higher proportion of *Bacillus* and *Mesorhizium* (Fig. 3), indicating that the Firmicutes probably involved in the nutrients uptake and plant metabolism, which could explain the majority of beneficial biocontrol-microbiota belong to this phylum in the root environment (Silvina et al. 2018).

We have demonstrated the prevalent role of organ niche in shaping the assembly and composition of the endosphere microbiome, and PERMANOVA for beta diversity based on the combined data from the organ niche and agricultural practice experiments demonstrated that plant organ niche had a significant impact on the endosphere microbial communities of tomato. Bacterial communities varied among different plant development stages, and numerous reports showed that rice genotype influenced the root microbiota construction (Wei et al. 2020). Salt-accumulating halophyte *S. European* would depend on microbiota, which promoting growth in saline conditions (Sun et al. 2008). Plants not only actively influence the microbiome structure in diverse niches by metabolites (Zhao et al. 2015), but also increase the abundance of beneficial communities at specific growth periods (Romero et al. 2014).

In summary, this study provided a comprehensive view of the organ niche and agricultural practice factors shaping the endophyte bacterial communities associated with tomato under greenhouse. Some beneficial endophyte bacterial strains have been isolated in this study and their functions in promoting growth and health will be studied in the future. These efforts will provide an important clue for the application of beneficial endophyte bacteria into tomato agricultural production. The interaction between the plant and related microbiota research could pave the way for technologies to modulate the plant microbiota that increase crop productivity and resist plant pathogen infection.

Conclusion

Tomato endophyte microbiota have a distinct structure in different plant development stage. *Bacillus*.spp were enriched seeding stage and decreased in the fruiting stage while *Mesorhizobium* increased during in the fruiting stage. Organ niche had a significant impact on the endosphere microbial communities of tomato.

Declarations

Acknowledgements

Not applicable.

Authors' contributions

ZZY designed the research, carried out the experiment, and drafted the manuscript. ZYB improved the writing of the manuscript. ZZQ, LYZ and WYQ revised the manuscript. All authors have read and approved the final manuscript.

Availability of data and materials

All data analyzed during this study are included in this published article and its supplementary information files.

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Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that there is no competing interest.

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Figures

Figure 1

Rarefaction curves for bacterial OTUs, clustering at 97 % rRNA sequence similarity. T1ORGR: organic system root endophyte in the seeding stage, T2ORGR: organic system root endophyte in the flowering stage, T3 ORGR: organic system root endophyte in the fruiting stage, T4ORGR: organic system root endophyte in the harvesting stage. T1CONR: conventional system root endophyte in the seeding stage, T2CONR: organic system root endophyte in the flowering stage, T3 CONR: organic system root endophyte in the fruiting stage, T4CONR: organic system root endophyte in the harvesting stage. T1ORGS: organic system stem endophyte in the seeding stage, T2ORGS: organic system stem endophyte in the flowering stage, T3 ORGS: organic system stem endophyte in the fruiting stage, T4ORGS: organic system stem endophyte in the harvesting stage. T1CONS: conventional system stem endophyte in the seeding stage, T2CONS: conventional system stem endophyte in the flowering stage, T3 CONS: conventional system stem endophyte in the fruiting stage, T4CONS: organic system stem endophyte in the harvesting stage.

Figure 2

Venn diagram showing the shared OTUs among the 80 samples. TIORGR: organic system root endophyte in the seeding stage, T2ORGR: organic system root endophyte in the flowering stage, T3 ORGR: organic system root endophyte in the fruiting stage, T4ORGR: organic system root endophyte in the harvesting stage. TICONR: conventional system root endophyte in the seeding stage, T2CONR: organic system root endophyte in the flowering stage, T3 CONR: organic system root endophyte in the fruiting stage, T4CONR: organic system root endophyte in the harvesting stage. TIORGS: organic system stem endophyte in the seeding stage, T2ORGS: organic system stem endophyte in the flowering stage, T3 ORGS: organic system stem endophyte in the fruiting stage, T4ORGS: organic system stem endophyte in the harvesting stage. TICONs: conventional system stem endophyte in the seeding stage, T2CONS: conventional system stem endophyte in the flowering stage, T3 CONS: conventional system stem endophyte in the fruiting stage, T4CONS: organic system stem endophyte in the harvesting stage.

Figure 3

3A Distribution of the bacteria from the endosphere of tomato plants at the phylum level. Fig 3B Distribution of the bacteria from the endosphere of tomato plants at the genus level. TIORGR: organic system root endophyte in the seeding stage, T2ORGR: organic system root endophyte in the flowering stage, T3 ORGR: organic system root endophyte in the fruiting stage, T4ORGR: organic system root endophyte in the harvesting stage. T1CONR: conventional system root endophyte in the seeding stage, T2CONR: organic system root endophyte in the flowering stage, T3 CONR: organic system root endophyte in the fruiting stage, T4CONR: organic system root endophyte in the harvesting stage. TIORGS: organic system stem endophyte in the seeding stage, T2ORGS: organic system stem endophyte in the flowering stage, T3 ORGS: organic system stem endophyte in the fruiting stage, T4ORGS: organic system stem endophyte in the harvesting stage. T1CONS: conventional system stem endophyte in the seeding stage, T2CONS: conventional system stem endophyte in the flowering stage, T3 CONS: conventional system stem endophyte in the fruiting stage, T4CONS: organic system stem endophyte in the harvesting stage.

4A

4B

Figure 4

4A. OTU bacterial Shannon index for four different plant development time. Fig. 4B. OTU bacterial Shannon index for four different treatments. treatments. CONR: conventional system root endophyte, CONS: conventional system stem endophyte, ORGR: organic system root endophyte, ORGS: organic system stem endophyte. (* denote significant, $p < 0.05$; ** denote extremely significant, $p < 0.01$). Fig. 4B. OTU bacterial Shannon diversity index for four different development stage of tomato. T1: seeding stage (March 2019), T2: flowering stage (May 2019), T3: fruiting stage (June 2019), T4: harvesting stage (July 2019)

Figure 5

5A. PCoA of bacterial microbiota using Bray–Curtis distance for four different treatment. Fig 5B. PCoA of bacterial microbiota using Bray–Curtis distance for four different plant development stage. CONR: conventional system root endophyte, CONS: conventional system stem endophyte, ORGR: organic system root endophyte, ORGS: organic system stem endophyte. T1: seeding stage (March 2019), T2: flowering stage (May 2019), T3: fruiting stage (June 2019), T4: harvesting stage (July 2019) 5C. PCoA of bacterial

microbiota using Bray–Curtis distance for different organ in seeding stage (T1). Fig 5D. PCoA of root bacterial microbiota using Bray–Curtis distance for different agricultural practices in seeding stage (T1). Fig 5E. PCoA of stem bacterial microbiota using Bray–Curtis distance for different manipulation in seeding stage (T1). CONR: conventional system root endophyte, CONS: conventional system stem endophyte, ORGR: organic system root endophyte, ORGS: organic system stem endophyte. T1: seeding stage (March 2019) 5F. PCoA of bacterial microbiota using Bray–Curtis distance for different organ in flowering stage (T2). Fig 5G. PCoA of root bacterial microbiota using Bray–Curtis distance for different agricultural practices in flowering stage (T2). Fig 5H. PCoA of stem bacterial microbiota using Bray–Curtis distance for different manipulation in flowering stage (T2). T2: flowering stage (May 2019) 5I. PCoA of bacterial microbiota using Bray–Curtis distance for different organ in fruiting stage (T3). Fig 5J. PCoA of root bacterial microbiota using Bray–Curtis distance for different agricultural practices in fruiting stage (T3). Fig 5K. PCoA of stem bacterial microbiota using Bray–Curtis distance for different manipulation in fruiting stage (T3). CONR: conventional system root endophyte, CONS: conventional system stem endophyte, ORGR: organic system root endophyte, ORGS: organic system stem endophyte. T3: fruiting stage (June 2019) 5L. PCoA of bacterial microbiota using Bray–Curtis distance for different organ in fruiting stage (T4). Fig 5M. PCoA of root bacterial microbiota using Bray–Curtis distance for different agricultural practices in fruiting stage (T4). Fig 5N. PCoA of stem bacterial microbiota using Bray–Curtis distance for different manipulation in fruiting stage (T4). CONR: conventional system root endophyte, CONS: conventional system stem endophyte, ORGR: organic system root endophyte, ORGS: organic system stem endophyte. T4: harveating stage (June 2019)

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