



Plant cultivars imprint the rhizosphere bacterial community composition and association networks



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ABSTRACT

Rhizosphere associated microbiota is of the central importance for modulating plant growth and health. To comprehensively understand the genetic principles governing the composition and co-occurrence patterns of the rhizosphere microbiota, the bacterial communities in the rhizospheres of 12 rabbiteye blueberry (RB) cultivars along with their counterparts in the blackberry rhizosphere and bulk soil were characterized to assess the relative influence of edaphic properties and plant cultivars. The composition and network structure of bacterial community were examined using Illumina sequencing of 16S rRNA gene, coupled with co-occurrence networks analysis. The diversity and composition of rhizosphere bacteria community depended more on the interactions with the soil environment (pH and organic carbon) than with the host cultivars. The bacterial assemblages within the blueberry cultivars clearly clustered into three groups (BRI, BRII and RBIII). The bacterial community composition in RBIII, with a higher abundance of Gammaproteobacteria but a lower abundance of Alphaproteobacteria and Actinobacteria, remarkably differed from that in BRI and BRII. *Rhizobiales* and *Pseudomonadaceae* predominated in the obtained rhizosphere core microbiota within the plant cultivars. The rhizosphere from the plant cultivars exerted substantial effects on bacterial association networks and putative keystone species. Intra and inter-phyllum/class co-occurrence in blueberry networks higher than expected by chance was induced by their common ecological niche differentiation or synergistic relationships. Taken together, a comprehensive understanding of the rhizosphere associated bacterial community structure and interaction networks is imperative to elucidate the biological mechanisms guiding bacterial assembly in the rhizosphere.

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1. Introduction

The plant rhizosphere contains an overwhelming number of microorganisms involved in critical processes that substantially modulate plant physiology and morphology, improve plant growth through the production of phytohormones, and serve as

protectants against phytopathogens (Philippot et al., 2013). Plants invest a huge amount of root exudates to provide sources of carbonaceous compounds for nurturing their rhizosphere microbiota (Bulgarelli et al., 2013). Physicochemical gradients and varying biochemical activities in the space encompassing roots provide a basis for the differentiation of the rhizosphere microhabitats that underlie complex microbe-microbe interactions and consequently orchestrate different microbial diversity and community compositions. Plants markedly vary in their rhizosphere microenvironments and presumably select a subset of microbes for specific functions (Bulgarelli et al., 2012). The core microbiota may have a

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strong ability to resist perturbations, while specific microorganisms respond rapidly to changing environmental conditions. The identified core microbiota in the roots of the tested *Arabidopsis thaliana* species comprised *Actinomycetales*, *Burkholderiales*, and *Flavobacteriales*, members of which are known to promote plant growth and health (Schlaeppli et al., 2014). The well-studied rhizosphere effect describes that the rhizosphere indigenous microbial community structure often remarkably differs across host species (Berendsen et al., 2012) and among genotypes within a single species (Bokulich et al., 2014). Recent investigations conducted with the reference plant *Arabidopsis thaliana* demonstrate that the host cultivars (genotypes) mediate a weak but measurable impact on the root-associated microbiota (Lundberg et al., 2012). Consequently, unraveling the interactions between host plants and their intimately related microbiota and identifying the plant alleles controlling these associations will open up new avenues to illustrate the biological mechanisms driving bacterial community assembly in the rhizosphere.

An ecological network usefully represents various biological interactions in an ecosystem where species are associated by complicated positive (e.g., commensalism and mutualisms) and negative (e.g., predation and competition) interactions (Chow et al., 2014). Community assembly rules are intriguing for microbial ecologists due to the lack of knowledge about microbial co-occurrence patterns. An in-depth investigation of co-occurrence networks is crucial to understand the underlying principles of the microbial community assembly and to identify possible keystone populations in community (Lynch and Neufeld, 2015). The rapid advance of high-throughput sequencing has provided revolutionary tools for analyzing the diversity and structure of the rhizosphere microbial community (Donn et al., 2015), yet these fundamental approaches have simultaneously left many unanswered questions regarding the potential cross-talk of rhizosphere microbial populations (Cardinale et al., 2015). Co-occurrence networks are increasingly used to infer linkages between microbial groups that jointly build up the complex and diverse community characteristics of oceans (Steele et al., 2011), freshwater (Eiler et al., 2012), streams (Widder et al., 2014), activated sludge (Ju et al., 2014), and soils (Menezes et al., 2014). Documenting inter-taxa and intra-taxa associations across the complex microbial communities may help to predict the functional roles, habitat affinities, and shared physiologies that can guide more focused studies or experimental settings (Cardinale et al., 2015). Hitherto, the questions remain open as to whether plant cultivars leave an imprint on the changes in the rhizosphere bacterial association networks.

The geographical area of blueberry cultivation has expanded dramatically from the traditional regions in the United States and Canada to Europe, central Chile, New Zealand/Australia, Japan, and most currently China (Retamales and Hancock, 2012). Blueberry can be considered as a good model to evaluate the relative contribution of soil characteristics and plant cultivars on the rhizosphere microbiome. Here, we hoped to gain insight into the ecological process of bacterial community assembly and selection in the rhizosphere. For this purpose, we presented a systematic framework for host–microbiota diversification and networks among 12 blueberry cultivars grown under field conditions. In parallel, the blackberry rhizosphere soil was collected to compare inter- with intra-species effects on rhizobacterial diversity. The 16S rRNA gene amplicon sequencing, coupled with co-occurrence networks analysis, was used to explore the bacterial community structure and compare associations within the tested blueberry cultivars. We hypothesized that soil properties and plant cultivars cooperatively shaped the variations in bacterial diversity and networks in the rhizosphere. Furthermore, we expected to discover core rhizosphere microbiota that was conserved within plant cultivars.

Overall, the systematic survey of the rhizosphere microbiota was particularly important for understanding casual relations between plants and soil biota. The network perspectives on ecology were used to map the pathways of potential interactions between bacteria and uncover deterministic processes shaping bacterial assembly.

2. Materials and methods

2.1. Sampling site and strategy

Soil samples were collected from twelve rabbiteye blueberry (*Vaccinium ashei* Reade) cultivars (RB) growing side-by-side and one blackberry (*Rubus* spp.) cultivar 'Hull' (HB) at the same growth stage (post-harvest stage) in 2014. The blueberry varietal types were developed from complex hybridization (Table S1). On the basis of previously established genotypic data (Bian et al., 2014), the phylogenetic structure of twelve blueberry cultivars in this study showed the intra-specific levels of stratification. The RB cultivars within each group were more similar than those in different groups. The blueberry and blackberry cultivars from the U.S. has been planted and intermingled (distance between plants: 4 m, distance between rows: 1.5 m) in the field parcel since 1998. The collection site was located in Lishui, Nanjing, China (31°65' N, 119°02' E). The region has a subtropical humid monsoon climate with an annual average temperature and precipitation of 16.1 °C and 1053 mm, respectively. The soil sampling site had a planting area of 60 m × 18 m, where was previously planted to *Camellia sasanqua*. Before the blueberry and blackberry seedling, the plot was consistently plowed and homogenized to minimize variability in soils. All blueberry and blackberry cultivars were grown in the same soil under conventional practices in the consistent way. The pedotaxon at the sampling site was classified as clay vertic-gleyic-stagnic anthrosol in Chinese Soil Taxonomy and Hydragric Anthrosols in the World Reference Base for Soil Resources (WRB classification). Clean cultivation, sheep manure application, hand weeding and free pesticide were conventional practices for blueberry and blackberry cultivation in this region. Clean cultivation was a management system with repeated weeding during plant growth. The sheep manure was placed annually in 25-cm deep holes at four random points below the tree canopy. The dose of manure was calculated from the blueberry demand for nitrogen in this region. Three plants per blueberry and blackberry cultivar were available for rhizosphere soil collection. When sampling the rhizosphere soils, we avoided collecting the roots near the positions with fresh manure. Five rhizosphere soil samples were randomly collected from individual plant at a depth of 0–20 cm using a clean spade, and then composited into a single sample. All soil samples were placed on ice and immediately transported to the laboratory. After shaking off the loosely adhering soil, 50 g of the tightly adhering rhizosphere soil was collected with a sterile brush, passed through a 4-mm sieve, homogenized and processed for soil properties analysis and bacterial community profiling. The blackberry rhizosphere soil was collected to compare inter- with intra-species effects on the diversity and composition of rhizosphere bacteria community. Bulk soil was sampled to provide the original information on soil characteristics and bacterial community composition without planting and fertilization.

2.2. Soil chemical properties and blueberry fruit yield

Soil chemical properties were detected according to the procedure described by Lu (2000). Soil pH was determined using a glass electrode in a 1:2.5 soil:water solution (w/v). Soil organic carbon (SOC) content was determined by wet digestion using the

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