Plant Soil (2021) 466:81–99
https://doi.org/10.1007/s11104-021-05036-2

REGULAR ARTICLE

Rice domestication influences the composition and function of the rhizosphere bacterial chemotaxis systems

Yu Sun · Lei Tian · Jingjing Chang · Shaohua Shi · Jianfeng Zhang · Hongwei Xie · Yaohui Cai · Dazhou Chen · Eiko E. Kuramae · Johannes A. van Veen · Weiqiang Li · Lam-Son Phan Tran · Chunjie Tian

Received: 17 October 2020 / Accepted: 3 June 2021 / Published online: 15 June 2021

Abstract

Aims Specific soil bacteria can sense and respond to the selective rhizosphere recruitment of root exudates using unique systems of chemotaxis that mediate plant-microbe and microbe-microbe interactions. This study investigates how the bacterial chemotaxis systems have been impacted by selection during the domestication of rice (*Oryza* species).

Methods Shotgun metagenomic sequencing and 16S rRNA gene amplicon sequencing were performed to investigate the bacterial chemotaxis systems and chemotactic bacteria in the rhizospheres of wild and cultivated rice. Metabolomics analysis was performed to examine the root metabolites of different accessions of rice.

Results The bacterial chemotaxis genes exhibited a higher abundance in the rhizospheres of wild rice than cultivated rice, and that the compositional profile of chemotaxis genes was distinctly different between types of rice. Differential selection of chemotaxis systems was

Responsible Editor: Luz E. de-Bashan.

Y. Sun · L. Tian · J. Chang · S. Shi · C. Tian (✉)
Key Laboratory of Mollisols Agroecology, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102, China
e-mail: tiancj@iga.ac.cn

J. Chang · E. E. Kuramae
Ecology and Biodiversity, Institute of Environmental Biology, Utrecht University, 3584 CH Utrecht, the Netherlands

J. Zhang
College of Life Science, Jilin Agricultural University, Changchun 130118, China

H. Xie · Y. Cai · D. Chen
Jiangxi Super-rice Research and Development Center, National Engineering Laboratory for Rice, Nanchang 330001, China

E. E. Kuramae · J. A. van Veen
Department of Microbial Ecology, Netherlands Institute of Ecology NIOO-KNAW, 6708 PB Wageningen, the Netherlands

W. Li (✉)
Institute of Plant Stress Biology, State Key Laboratory of Cotton Biology, Department of Biology, Henan University, Kaifeng 475001, China
e-mail: weiqiangli@henu.edu.cn

L.-S. P. Tran
Institute of Research and Development, Duy Tan University, Da Nang 550000, Vietnam

L.-S. P. Tran (✉)
Institute of Genomics for Crop Abiotic Stress Tolerance, Department of Plant and Soil Science, Texas Tech University, Lubbock, TX 79409, USA
e-mail: son.tran@ttu.edu

at least partially driven by changes in the metabolite profiles of rice roots that were affected by domestication. A core group of chemotactic bacteria was also identified, and specific chemotactic bacteria were found to function as hub taxa in the rhizosphere bacterial community.
Conclusion The present study provides novel insights into the composition and function of the bacterial chemotaxis systems in the rhizospheres of wild and domesticated rice. It also provides a new perspective on the impact of rice domestication on the assembly of rhizomicrobiome.

Keywords Rice domestication · Rhizosphere · Bacterial chemotaxis systems · Root metabolites · Bacterial community

Introduction

Rhizosphere microbiota play important roles in plant growth and stress adaptation by promoting nutrient acquisition (Jacoby et al. 2017), providing protection against pathogens (Kwak et al. 2018), and regulating host immunity (Berendsen et al. 2018). Rhizo-deposits (root exudates) have been reported to enable plants to shape and sustain their rhizomicrobiomes (Philippot et al. 2013). Plants can selectively recruit specific bacteria to their rhizosphere from the microbial community of the bulk soil by secreting a variety of root-derived products, including hormones, flavonoids, carbonic acids, amino acids and sugars (Badri et al. 2013; Hu et al. 2018; Mostofa et al. 2018). Little is known, however, about how specific bacteria respond to these biochemical signals. Chemotaxis, which is the ability of motile bacteria to change their direction of movement in responses to environmental stimuli, has been shown to provide motile bacteria with a competitive advantage in reaching the rhizosphere (Scharf et al. 2016). Abundant experimental data have demonstrated that chemotactic bacteria can sense and migrate along a chemical gradient formed by root exudates in the rhizosphere, and that their chemotactic response plays a major role in regulating plant-microbe interactions (Raina et al. 2019). For example, the chemotactic response of *Rhizobium* toward flavonoids exuded by legumes is regarded as the initial step in establishing a symbiosis (Cooper 2007). The chemotactic responses of two genera of plant growth-promoting bacteria, *Bacillus* and *Pseudomonas*, toward organic acids exuded by plant hosts regulate their colonization on root surfaces (Jin et al. 2019; Oku et al. 2014). The infection of plants by *Ralstonia solanacearum* is also regulated by the chemotactic responses of this bacterial pathogen to root exudates (Hasegawa et al. 2019). Microbe-microbe interactions involving chemotaxis also play a major selective role in the sculpting of microbial assemblages as well. For example, volatile fatty acids secreted by *Clostridium cellulovorans* can induce chemotaxis in *Rhodopseudomonas palustris* and affect their interaction (Lu et al. 2016). Thus, chemotaxis appears to represent a critical mechanism utilized by specific soil bacteria to actively respond to both plant host recruitment efforts and microbial interactions. Therefore, chemotactic bacteria may have a profound effect on shaping the assembly of the rhizomicrobiome.

Chemotaxis systems have been well characterized at the molecular level in several model bacterial organisms, including *Escherichia coli* and *B. subtilis* (Parkinson et al. 2015; Rao et al. 2008). The analyses of these model organisms revealed variation in the composition of the identified chemotaxis systems (Tindall et al. 2012) with a total of 11 components being identified (Parkinson et al. 2015; Wuichet and Zhulin 2010). The signal transduction system within these systems generally operates as illustrated in Fig. 1. Briefly, chemotactic signals, such as root exudates, are initially detected by methyl-accepting chemotaxis proteins (MCPs) and transmitted to chemotaxis protein A (CheA), a histidine kinase that is linked to MCPs by CheW or CheV adaptor proteins. The autophosphorylation level of CheA is regulated by signal binding, and phosphorylated CheA subsequently transmits the phosphoryl group to its response regulator CheY. Finally, phosphorylated CheY binds to the flagellar motor, changing its direction of rotation. CheB, a methylesterase, also receives a phosphoryl group from CheA, and phosphorylated CheB competes with CheR, a methyltransferase, in regulating the methylation state of MCPs. This system enables adjustments to the binding affinity of MCPs with chemotaxis signals, thus mediating the response of the chemotaxis system. In addition to the described Che proteins, CheC, CheX and CheZ function as phosphatases that dephosphorylate phosphorylated CheY; and CheD, a deamidase, acts on MCPs and CheC. Notably, CheC also

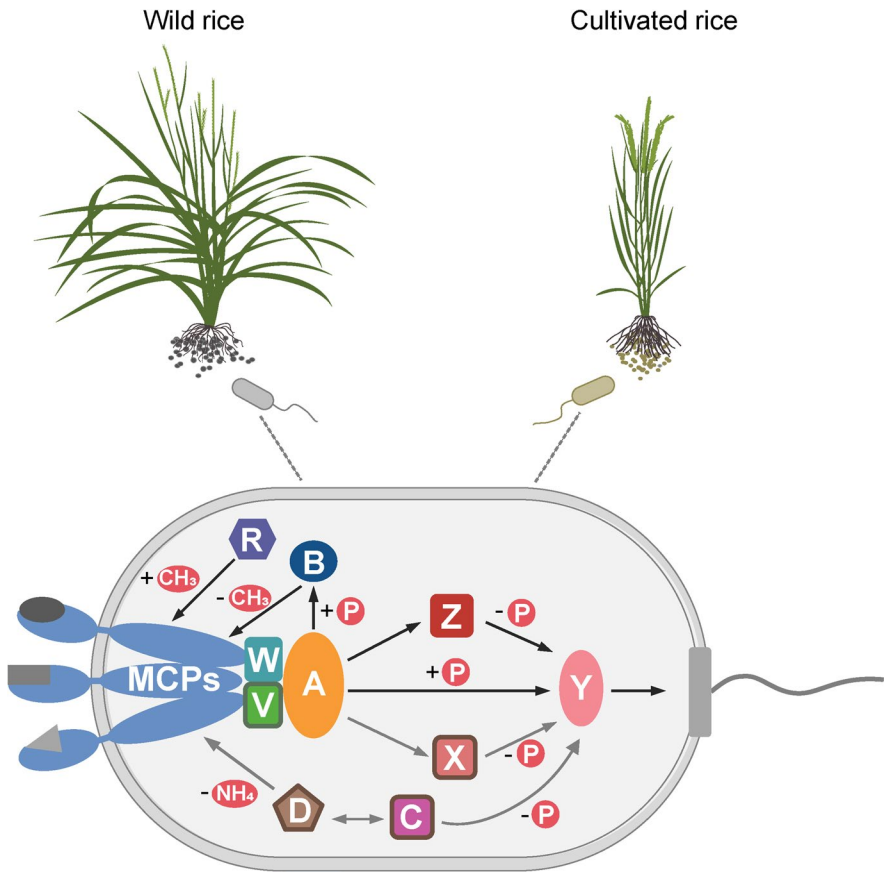

Fig. 1 A model of signal transduction in the chemotaxis systems in the rhizosphere of rice. Chemotaxis is induced in chemotactic bacteria by rice root exudates (represented by dots near the roots), which function as chemotactic signals. A summary model illustrates the organization of bacterial chemotaxis systems based on current knowledge derived from *Escherichia coli*. The components with the brown frames and the interactions represented by grey arrows, however, are not present in *E. coli*. The model is adopted from the publication by Wuichet and Zhulin (2010) with some modifications. MCPs, methyl-accepting chemotaxis proteins; V and W, chemotaxis protein (Che) V and CheW adaptor proteins, respectively; A, CheA histidine kinase; Y, CheY response regulator; B, CheB methylesterase; R, CheR methyltransferase; C, X and Z, CheC, CheX and CheZ phosphatases, respectively; D, CheD deamidase; P, phosphoryl group; CH_3, methyl group; NH_4^+, ammonium group. The gray ellipse, rectangle and triangle binding to MCPs represent different chemotactic signals

regulates the binding of CheD to MCPs. Increasing evidence indicates that chemotaxis genes are widespread in the genomes of soil bacteria (Wuichet and Zhulin 2010). Only a few studies, however, have studied these genes at the community level in soil ecosystems. Xu et al. (2018) reported that chemotaxis genes were enriched in the rhizospheres of *Citrus* species compared with the surrounding bulk soil. Buchan et al. (2010) analyzed *cheA* genes in the rhizosphere bacterial communities of wheat (*Triticum aestivum*) and cowpea (*Vigna unguiculata*) using terminal restriction fragment length polymorphism, and found that the profiles were distinct for each of the two crops. The ecological adaptation and evolution of chemotaxis genes in soil bacteria at the community level have not been determined. Notably, the composition and function of chemotaxis systems in the rhizospheres of rice (*Oryza* species) and other crops have not been systematically investigated.

Rice is staple food crop that feeds nearly half of the world's population (Khush 2005), and the domestication of rice has been regarded as a major accomplishment in the history of mankind (Kovach et al. 2007). The widely-grown Asian cultivated rice (*O. sativa*) has two main varietal groups: *japonica* (*O. sativa*

ssp. *japonica*) and *indica* (*O. sativa* ssp. *indica*), which are considered to have been derived from the common wild rice (*O. rufipogon*) and/or Indian wild rice (*O. nivara*) (Choi et al. 2017). African cultivated rice (*O. glaberrima*), which is indigenous to Africa, is considered to have been independently domesticated from African wild rice (*O. barthii*) (Wang et al. 2014). The domestication of rice involved gene selection to enhance desirable traits, and significant changes in field management practices to optimize yield. These major changes may have also impacted the interactions that occur between rice and rhizosphere microbes (Kim et al. 2020). A study of several rice accessions reported that the rhizosphere bacterial communities of wild and cultivated rice exhibited significant differences (Shenton et al. 2016). It is also assumed that plant domestication may have caused significant alterations in root exudation profiles, which in turn would affect the composition and function of the rhizomicrobiome (Perez-Jaramillo et al. 2016).

Given the potential role of chemotaxis in regulating the assembly of the rhizomicrobiome, it is important to study the composition and function of chemotaxis systems at the community level in wild and domesticated rice accessions. In a previous study, the shotgun metagenomic sequencing has been used to investigate the function of the whole microbial rhizosphere communities (Tian et al. unpublished data). In the present study, the abundance and compositional profile of chemotaxis genes in the rhizospheres of diverse rice accessions were assessed by re-analyzing the shotgun metagenomic sequencing data. Subsequently, a metabolomic analysis of root metabolites was conducted, and the resulting metabolomic data were analyzed together with the metagenomic sequencing data to determine potential correlations between chemotaxis genes and root metabolites. In addition, 16S rRNA gene amplicon sequencing was conducted to investigate the roles of specific chemotactic bacteria in the bacterial rhizosphere community. We hypothesized that the bacterial chemotaxis systems would be differentially distributed in the rhizospheres of wild and cultivated rice accessions and the different selection pressure exerted by host plants might be associated with their root metabolites. We also hypothesized that the specific chemotactic bacteria could contribute to the assembly of rhizosphere bacterial communities of wild and cultivated rice.

Material and methods

Plant materials and site description

Five wild and six cultivated rice accessions were used in this study. The five accessions of wild rice were assigned to three types of wild rice: i) African wild rice (*O. barthii*) IRGC 106238; ii) common wild rice (*O. rufipogon*) IRGC 106452 and 106,286; and iii) Indian wild rice (*O. nivara*) IRGC 86655 and 88,949. The six accessions of cultivated rice were also assigned to three types of cultivated rice: i) African cultivated rice (*O. glaberrima*) LM8 and WH20; ii) Asian cultivated rice variety *japonica* (*O. sativa* ssp. *japonica*) Jiangxi and Daohuaxiang; and iii) Asian cultivated rice variety *indica* (*O. sativa* ssp. *indica*) 106 and Meitezhen (Tian et al. unpublished data). The seeds of the wild rice accessions and cultivated rice accessions were kindly provided by the International Rice Research Institute (Los Baños, Laguna, Philippines) and the Jiangxi Academy of Agricultural Sciences (Nanchang, Jiangxi Province, China), respectively.

The experiment was conducted using a randomized block design at the rice experimental station (18°19' N, 109°27′ E, San'ya, Hainan Province, China), which has a tropical maritime monsoon climate. The values for soil characteristics have been described in a comparative study of the rhizosphere fungal communities of wild and cultivated rice accessions (Chang et al. 2021).

Sample collection

Rhizosphere samples were collected at the flowering stage of rice (Tian et al. unpublished data). Plants of each accession of wild and cultivated rice were randomly collected from five locations within a plot, with distances of 20 cm between the sampling locations. Samples collected from the five locations within a plot were pooled and treated as a single biological replicate. Five biological replicates from five plots were harvested for each accession of rice (except common wild rice IRGC 106452, for which four biological replicates were harvested) and treated as a single varietal replicate. Each plant was shaken to remove soil that was loosely adhered to roots. Roots were then submerged in tubes containing 5 mL of distilled water, and the tubes were vortexed to collect the

rhizosphere soil that was tightly attached to the roots (0-2 mm) (Edwards et al. 2015). Approximately 1 g of soil was obtained from each biological replicate after centrifugation. Collected samples were stored at 4 °C. Rice roots from each biological replicate were also collected by thoroughly washing them to remove all remaining soil particles. Clean root samples were transferred to tubes and stored at −80 °C.

DNA extraction

Genomic DNA was extracted from the rhizomicrobiome present in 0.5 g of soil using a FastDNA SPIN Kit For Soil (MPBio, Santa Ana, CA, USA) according to the manufacturer's instructions. The concentrations of DNA in samples were quantified using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA).

High throughput sequencing and data analysis

Shotgun metagenomic sequencing and data analysis has been described in detail in Tian et al. (unpublished data). The chemotaxis genes were then identified and annotated using the automatic annotation server of the KEGG (Kyoto Encyclopedia of Genes and Genomes) (https://www.genome.jp/tools/kaas/) (Moriya et al. 2007).

The V3-V4 region of the bacterial 16S rRNA gene was amplified from the extracted DNA using the universal primer pair 341F (5′-CCTACGGGNGGC WGCAG-3′) and 806R (5′- GGACTACHVGGGTWT CTAAT-3′) incorporated with barcodes to obtain individual barcoded libraries. The libraries were then pooled into a single library at equal concentrations. Subsequently, 250-bp paired-end sequencing was performed using the Illumina Hi-Seq2500 platform.

The raw sequencing reads were then processed. Briefly, paired-end reads were joined into a complete sequence using FLASH 1.2.7 (Magoc and Salzberg 2011). Reads shorter than 300-bp and other low-quality reads were removed from the dataset using Trimmomatic 0.33 (Bolger et al. 2014). Chimeric sequences were identified and removed using UCHIME 4.2 (Edgar et al. 2011). The remaining high-quality reads were then clustered into operational taxonomic units (OTUs) based on 97% sequence identity using UPARSE 7.0.1001 (Edgar 2013). The most abundant sequence in each OTU was selected as the representative sequence and taxonomically classified using the Ribosomal Database Project classifier 2.2 against the SILVA database (Release128, https://www.arb-silva.de/).

Gas chromatography time-of-flight mass spectrometry (GC-MS) analysis of root metabolites.

Metabolites were extracted from 10 mg of each root sample according to the previously reported method (Lisec et al. 2006). GC-MS analysis of root metabolites of rice root samples was performed using the protocol described by Li et al. (2020a). The mass spectrometry data of root metabolites were then processed using ChromaToF 4.3 (LECO, St. Joseph, MI, USA) and LECO-Fiehn Rtx5 database (LECO, St. Joseph, MI, USA).

Data analysis and visualization

Multiple comparisons of chemotaxis gene abundance were carried out by one-way analysis of variance (ANOVA) (significance level, $p < 0.01$) in SPSS 17.0 (SPSS Inc., Chicago, IL, USA). Principal coordinates analysis (PCoA) and principal component analysis (PCA) were performed using the "vegan" package in R 3.6.2, and the statistical significance of the clustering patterns in ordination plots was determined using permutational multivariate analysis of variance (PERMANOVA). The differentially abundant chemotaxis genes (fold change >2) and differentially abundant root metabolites (fold change >1.4) between two groups (wild and cultivated rice accessions) were identified using the Welch's *t*-test in STAMP 2.1.3 with *p* values adjusted using the Benjamini-Hochberg method (Benjamini and Hochberg 1995; Parks et al. 2014). A correlation analysis between abundance of chemotaxis genes and abundance of root metabolites was performed with the "psych" package in R 3.6.2 using the pairwise Spearman's rank correlation. Heatmaps representing significant correlations (Spearman's $|\rho| > 0.8$, $p < 0.01$ for wild rice, Spearman's $|\rho| > 0.7$, $p < 0.01$ for cultivated rice because non-significant correlations were identified using the threshold of $|\rho| > 0.8$) were constructed using the "pheatmap" package in R 3.6.2. Significant differences in the abundance of chemotaxis genes and abundance of metabolites between wild and cultivated rice were evaluated using a Student's *t* test (significance level, $p < 0.01$) in SPSS 17.0.

The taxonomic annotation of chemotaxis genes was performed using BLASTx. The Venn diagram illustrating the taxa of chemotactic bacteria in and shared between wild and cultivated rice was constructed using the "VennDiagram" package in R 3.6.2. The correlation analyses of rhizosphere bacterial communities of wild and cultivated rice were performed using the pairwise Spearman's rank correlation based on the results of 16S rRNA gene-amplicon sequencing. Co-occurrence networks were visualized in Gephi 0.9.2 (Bastian et al. 2009), with only significant correlations represented in the network (Spearman's $|\rho| > 0.8$, $p < 0.01$ for both wild and cultivated rice). The topological properties of nodes were also analyzed and the hub taxa in the network were defined as nodes belonging to the top 2% of degree and betweenness centrality (Kim et al. 2020). Threshold values of degree/betweenness centrality for wild and cultivated rice networks were 13.5/535 and 3.5/35, respectively.

Results

Compositional shift in bacterial chemotaxis systems in the rhizospheres of wild and cultivated rice

Analysis of the metagenomic sequencing data revealed that the identified chemotaxis systems represented 11 functional KOs (KEGG Orthology) corresponding to different proteins, with each KO comprising dozens of orthologous genes. The abundance of chemotaxis genes was then analyzed to determine if any differences existed between the bacterial chemotaxis systems in the rhizospheres of wild and cultivated rice. Results showed that the rhizospheres of wild rice accessions in general had a significantly higher abundance of chemotaxis genes than the rhizospheres of cultivated rice accessions (Fig. 2). More specifically, the rhizosphere of African wild rice had the highest abundance of chemotaxis genes, while the rhizosphere of African cultivated rice had the lowest abundance of chemotaxis genes (Fig. 2).

PCoA was subsequently performed, based on the Bray-Curtis dissimilarity matrix calculated from the abundances of orthologous genes, to compare the composition of bacterial chemotaxis systems in the rhizospheres of wild and cultivated rice accessions. Samples of wild and cultivated rice accessions were separated across the first principal coordinate (Fig. 3a), suggesting that the compositional profiles of chemotaxis genes in the rhizospheres of wild and cultivated rice accessions were distinct. The six different types of wild and cultivated rice were identified in the PCoA plot to provide additional detail. Notably, separations within the three types of wild rice accessions, and a separation of African cultivated rice from the other two types of cultivated rice accessions, Asian cultivated rice variety *japonica* and *indica*, were observed (Fig. 3a and Table S1), indicating that differences in the chemotaxis systems also exist between different types of wild and cultivated rice accessions. Interestingly, a clear separation in the compositional profile of chemotaxis genes was also observed between the two common wild rice varieties (IRGC 106452 and 106,286) and between the two Indian wild rice varieties (IRGC 86655 and 88,949) (Fig. 3a and Table S1), suggesting the existence of varietal disparity within these wide species. Notably, no separations were observed among the three types of cultivated rice accessions (Fig. 3a and Table S1), indicating that the composition of the bacterial chemotaxis systems was similar within the cultivated rice accessions regardless of their African or Asian origin.

The specific genes responsible for the differences in the chemotaxis systems in the rhizospheres of wild and cultivated rice accessions were then subsequently identified. Approximately 30% of the genes identified as K03406 (*mcp*), K03412 (*cheB*) and K00575 (*cheR*), and more than 60% of the genes identified as K03407 (*cheA*) were shown to be differentially abundant in the rhizospheres of wild and cultivated rice accessions (Fig. S2 and Table S2). No differentially abundant genes were identified among the other seven functional KOs, including K03408 (*cheW*), K03409 (*cheX*), K03410 (*cheC*), K03411 (*cheD*), K03413 (*cheY*), K03414 (*cheZ*) and K03415 (*cheV*) (Table S2). The PCoA of the four differentially abundant KOs revealed that plots of all four of the KOs exhibited a clear separation between the wild and cultivated rice accessions across the first principal coordinate (Fig. 3b-e and Table S1). Clear separations within the three types of wild rice accessions were observed for all four of the KOs, and a separation

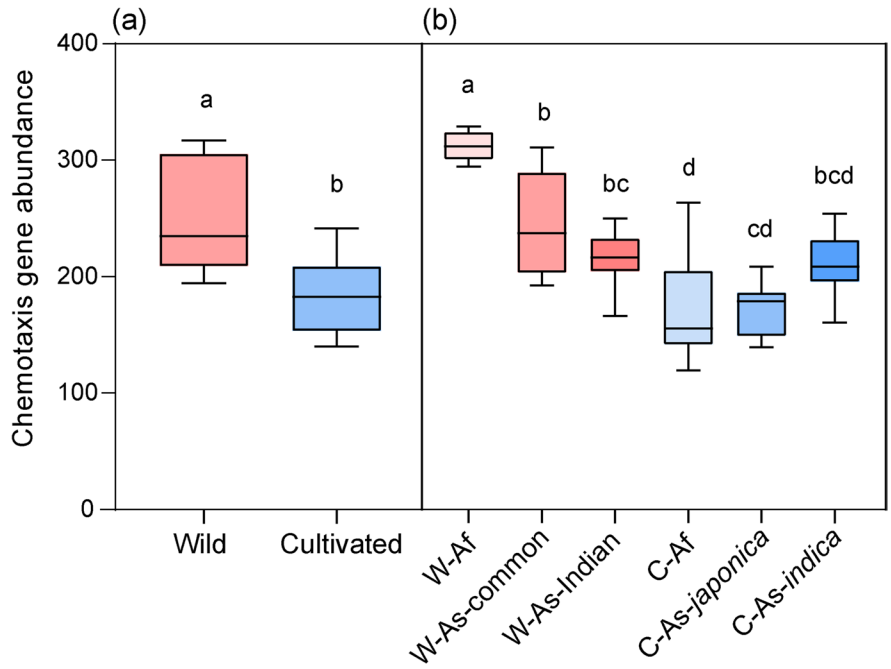

Fig. 2 Abundance of orthologous chemotaxis genes present in the rhizospheres of wild and cultivated rice accessions. (**a**) All rice accessions were separated into two groups: Wild ($n=3$ groups with 5, 9 and 10 biological replicates, respectively); Cultivated ($n=3$ groups with 10 biological replicates each). (**b**) All rice accessions were separated into six groups: W-Af ($n=5$ biological replicates); W-As-common ($n=9$ biological replicates); W-As-Indian, C-Af, C-As-*japonica* and C-As-*indica* ($n=10$ biological replicates). Levels of abundance represent transcripts per million values of orthologous chemotaxis genes. The boxplots represent the mean and 10th and 90th percentile, and the error bars indicate the standard deviation of the replicates. Bars with the same letter on top have non-significant differences (ANOVA, $p > 0.01$). W-Af: African wild rice IRGC 106238; W-As-common: common wild rice IRGC 106452 and 106,286; W-As-Indian: Indian wild rice IRGC 86655 and 88,949; C-Af: African cultivated rice LM8 and WH20; C-As-*japonica*: Asian cultivated rice variety *japonica* Jiangxi and Daohuaxiang; C-As-*indica*: Asian cultivated rice variety *indica* 106 and Meitezhen

of African cultivated rice from the other two types of cultivated rice accessions, Asian cultivated rice variety *japonica* and *indica*, was also noted for K03406, K03412 and K00575 but not for K03407 (Fig. 3b-e and Table S1). These results suggest that differences also exist in the distribution patterns of chemotaxis genes in the rhizospheres of different wild and cultivated rice accessions. It is worth noting that *mcp*, *cheA*, *cheB* and *cheR* are all associated with chemotaxis signal processing (Tindall et al. 2012). The compositions of rhizosphere bacterial communities of wild and cultivated rice accessions were also analyzed using PCoA based on Bray-Curtis dissimilarity matrix calculated from the relative abundances of bacterial genera identified by 16S rRNA gene amplicon sequencing. The results showed that there were significant differences in the composition of rhizosphere bacterial communities between wild and cultivated rice accessions (Fig. S1). Collectively, these data indicate that domestication of cultivated rice from wild rice exerted different selection pressures on bacterial chemotaxis systems in their associated rhizomicrobiomes, particularly on the components responsible for chemotaxis signal processing. This selection pressure has resulted in distinct differences in the composition of their respective chemotaxis systems.

Differences in the metabolite profiles of roots of wild and cultivated rice

A metabolomic analysis of roots associated with the rhizospheres of the five wild and six cultivated rice accessions was performed to determine if differences exist between their root metabolite profiles,

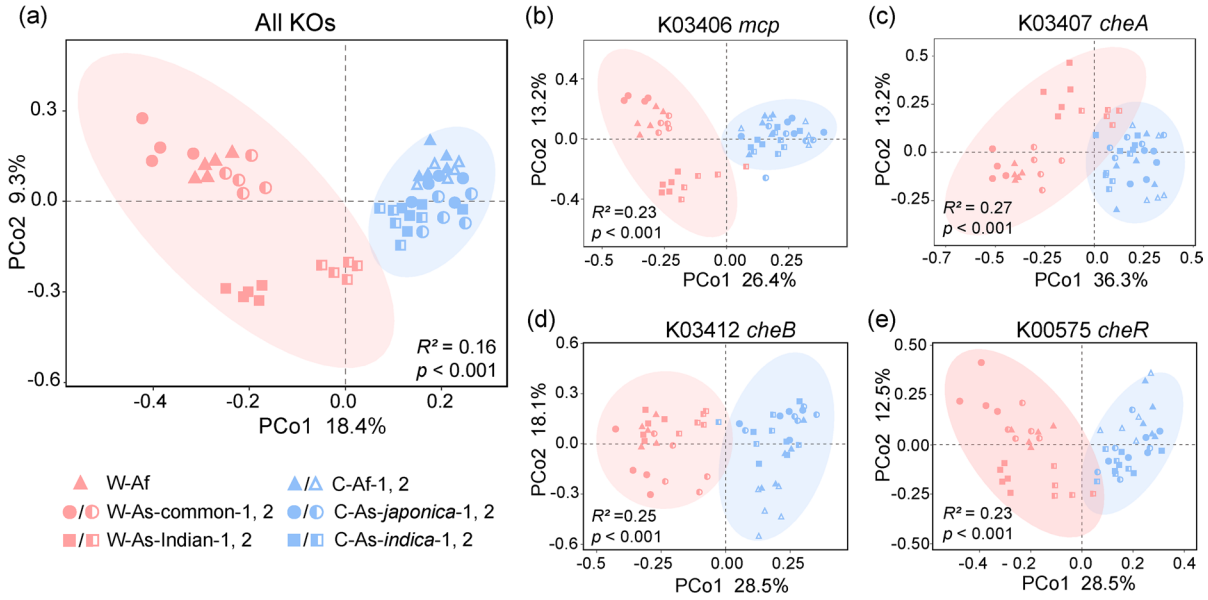

Fig. 3 Principal coordinate analysis (PCoA) of the functional KOs of the chemotaxis systems in the rhizospheres of wild and cultivated rice accessions. Variation of all functional KOs (**a**), K03406 (**b**), K03407 (**c**), K03412 (**d**) and K00575 (**e**) in the rhizospheres of wild and cultivated rice accessions PCoA was based on the Bray-Curtis dissimilarity matrix calculated from the relative abundance of orthologous genes. The 95% confidence ellipses are drawn in pink for the wild and blue for the cultivated rice accessions. Triangles, circles and squares of different colors represent different wild and cultivated rice accessions. W-Af: African wild rice IRGC 106238; W-As-common-1, 2: common wild rice IRGC 106452 and 106,286; W-As-Indian-1, 2: Indian wild rice IRGC 86655 and 88,949; C-Af-1, 2: African cultivated rice LM8 and WH20; C-As-*japonica*-1, 2: Asian cultivated rice variety *japonica* Jiangxi and Daohuaxiang; C-As-*indica*-1, 2: Asian cultivated rice variety *indica* 106 and Meitezhen

which might have resulted from domestication. The relative abundances of root metabolites were different in wild vs. cultivated rice accessions (Fig. 4a and Table S3). A total of 228 metabolites were identified collectively in the roots of wild and cultivated rice accessions (Fig. 4b and Table S3). The identified metabolites represented seven compositional categories, 'sugars', 'amino acids', 'alcohols', 'fatty acids', 'organic acids', 'phosphates' and 'others' (Fig. 4b and Table S3). For example, a higher abundance of 'sugars' and 'alcohols', but a lower abundance of 'amino acids' and 'organic acids' categories were detected in wild rice roots than in cultivated rice roots (Fig. 4a). Collectively, 123 of the 228 identified metabolites were found to be differentially abundant (fold change >1.4, $q < 0.01$) between wild and cultivated rice root samples (Fig. 4b and Table S3). Specifically, 9 metabolites in five compositional categories ('sugars', 'amino acids', 'alcohols', 'organic acids' and 'others') had higher abundance in wild rice roots, while the other 114 metabolites belonging to all seven compositional categories had higher abundance in cultivated rice roots (Fig. 4b and Table S3). These results revealed a remarkable difference in the root metabolite profile of wild vs. cultivated rice accessions.

The diversity of root metabolites was further analyzed by conducting a PCA of root metabolite profiles from wild and cultivated rice accessions. The resulting plot revealed that wild and cultivated rice accessions clearly clustered separately (Fig. 4c), providing further evidence that the root metabolite profile of wild rice accessions was distinct from that of cultivated rice accessions. In addition, separations within the three types of wild rice accessions and within the three types of cultivated rice accessions were observed (Fig. 4c and Table S4). Collectively, these results indicate that wild and cultivated rice accessions possess specific root metabolite profiles, which might be affected by domestication.

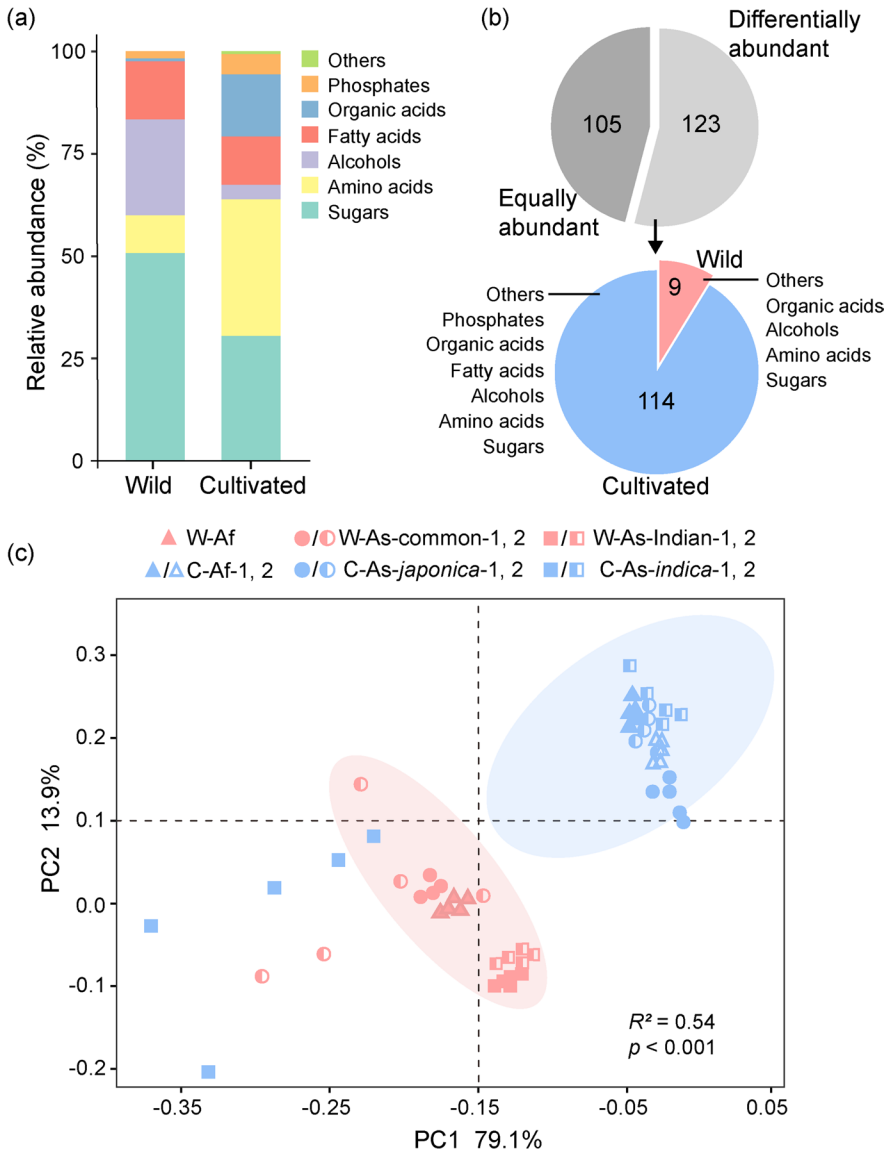

Fig. 4 Metabolomic analysis of roots of wild and cultivated rice accessions. (**a**) Relative abundance of different categories of root metabolites in wild and cultivated rice accessions. Root metabolites were classified into different groups and labeled accordingly. (**b**) Pie charts illustrating the number of differentially abundant metabolites in wild and cultivated rice within the different compositional categories. The differentially abundant root metabolites were identified by a comparison of wild and cultivated rice accessions (fold change >1.4, $q < 0.01$). (**c**) Principal component analysis (PCA) of root metabolites in wild and cultivated rice accessions. PCA was performed based on the relative abundance of root metabolites. The 95% confidence ellipses were drawn in pink for the wild rice and in blue for the cultivated rice accessions. The triangles, circles and squares in different colors represent different accessions of wild and cultivated rice. W-Af: African wild rice IRGC 106238; W-As-common-1, 2: common wild rice IRGC 106452 and 106,286; W-As-Indian-1, 2: Indian wild rice IRGC 86655 and 88,949; C-Af-1, 2: African cultivated rice LM8 and WH20; C-As-*japonica*-1, 2: Asian cultivated rice variety *japonica* Jiangxi and Daohuaxiang; C-As-*indica*-1, 2: Asian cultivated rice variety *indica* 106 and Meitezhen

Correlation between chemotaxis genes and root metabolites

Root metabolites secreted in the rhizosphere function as principal chemotactic signals (Buchan et al. 2010; Scharf et al. 2016), and our results revealed that chemotaxis genes responsible for chemotaxis signal processing are differentially abundant in wild and cultivated rice accessions (Fig. 3b-e). Therefore, we hypothesized that the distinctly different metabolite profiles present in the rhizosphere roots of wild and cultivated rice accessions (Fig. 4) are the driving force for the differential recruitment and selection of chemotactic bacterial communities and their associated chemotaxis systems. Thus, a correlation analysis between differentially abundant chemotaxis genes and root metabolites was conducted to provide evidence for this hypothesis.

Twelve chemotaxis genes that had higher abundance (fold change >2, $q < 0.01$) in the rhizospheres of the five

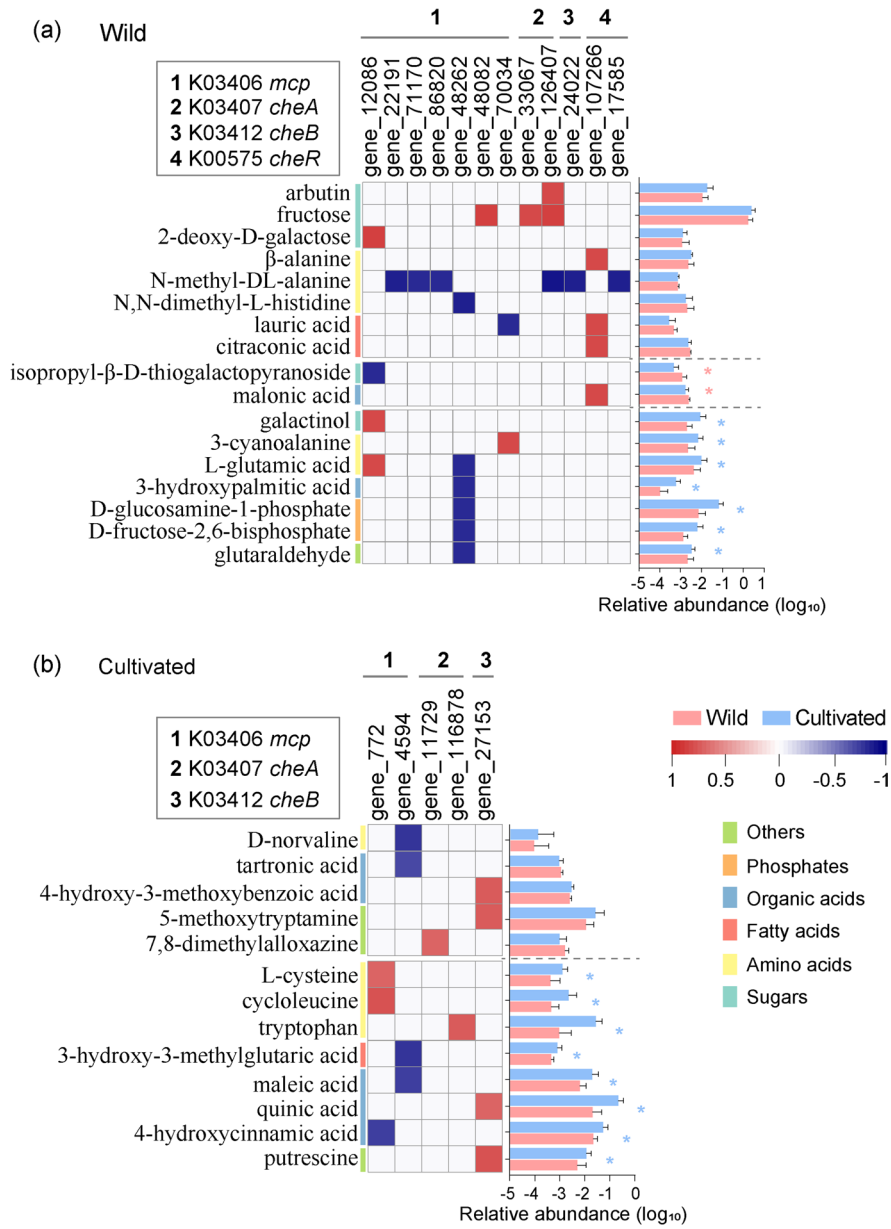

Fig. 5 Correlation analysis of chemotaxis genes and root metabolites. Heatmaps (left panels) displaying the correlation between chemotaxis genes and root metabolites in the rhizospheres of wild (**a**) and cultivated (**b**) rice accessions, and the relative abundance (right panels) of the root metabolites in wild (pink) and cultivated (blue) rice accessions. Root metabolites were grouped according to the different compositional categories. The threshold of $|\rho|$ is 0.8 for wild rice. The threshold of $|\rho|$ is 0.7 for cultivated rice. Red blocks represent significant positive correlations (Spearman's $\rho > 0$, $p < 0.01$) and dark-blue blocks represent significant negative correlations (Spearman's $\rho < 0$, $p < 0.01$). Error bars represent standard deviations of the replicates (Wild, $n = 3$ groups with 5, 9 and 10 biological replicates, respectively; Cultivated, $n = 3$ groups with 10 biological replicates each). Pink and blue asterisks (*) indicate that the metabolites had a higher relative abundance in the rhizospheres of wild and cultivated rice (Student's t test, $p < 0.01$), respectively, over the other group

accessions of wild rice than in those of cultivated rice exhibited significant correlations (Spearman's $|\rho| > 0.8$) with 17 root metabolites belonging to the categories 'sugars', 'amino acids', 'fatty acids', 'organic acids' and 'phosphates' (Fig. 5a and Fig. S2). For example, the abundance of fructose in the category 'sugars' had a significant positive correlation (Spearman's $\rho > 0.8$) with three genes classified as K03406 and K03407 (Fig. 5a), while N-methyl-DL-alanine within the category 'amino acids' had a significant negative correlation (Spearman's $\rho < 0.8$) with several genes classified as K03406, K03407, K03412 and K00575 (Fig. 5a). Notably, when the abundances of these 17 metabolites in wild and cultivated rice accessions were compared, the results surprisingly indicated that eight of the 17 had equal abundance in both types of accessions (Fig. 5a), while two and seven metabolites had higher abundance in wild and cultivated rice accessions, respectively, over the other group (Fig. 5a). More specifically, metabolites with lower abundance were significantly correlated with highly abundant chemotaxis genes in the rhizospheres of wild rice accessions.

Five chemotaxis genes and 13 root metabolites were found to be significantly correlated in the six cultivated rice accessions (Fig. 5b). Additionally, the general level of correlation represented by the Spearman's $|\rho|$ value (Spearman's $0.7 < |\rho| < 0.8$) was also lower (Fig. 5b). These results suggest that the selection pressures on bacterial chemotaxis systems exerted in cultivated rice might be different from those of wild rice. Five chemotaxis genes affiliated with three KOs (K03406, K03407 and K03412) were significantly correlated with 13 metabolites within the categories 'sugars', 'amino acids', 'fatty acids' and 'organic acids' (Fig. 5b). All of these five genes had higher abundance in the rhizospheres of cultivated rice accessions than in those of wild rice accessions (Fig. S2). Five out of the 13 metabolites were equally abundant in roots of both wild and cultivated rice accessions, while the other eight metabolites had higher abundance in the roots of cultivated rice accessions (Fig. 5b). In comparison with wild rice accessions, each metabolite in the cultivated accessions was significantly correlated (Spearman's $|\rho| > 0.7$) with only a single chemotaxis gene (Fig. 5a-b). For example, tartronic acid within the category 'organic acids' exhibited a significant negative correlation (Spearman's $\rho < 0.7$) with a gene belonging to KO K03406, while L-cysteine in the category 'amino acids' had significant positive correlation (Spearman's $\rho > 0.7$) with another gene classified as KO K03406. Notably, no overlaps were observed in the metabolites of wild and cultivated rice accessions that exhibited a significant correlation with chemotaxis genes. Collectively, these results indicate that specific root metabolites present in either the wild or cultivated rice accessions contribute to the differential selection of bacterial chemotaxis systems in their rhizospheres. Although selection could be affected by the surrounding environment, the differences in root metabolite profile between wild and cultivated rice accessions may partially contribute to the distinct composition of bacterial chemotaxis systems recruited from the array of chemotactic bacterial communities present in their rhizospheres.

Roles of the core groups of chemotactic bacteria in the rhizosphere bacterial communities in wild and cultivated rice accessions

The core groups of chemotactic bacteria in the rhizospheres of wild and cultivated rice accessions were investigated based on the hypothesis that chemotactic bacteria affect the assembly of the rhizomicrobiome. Differentially abundant chemotaxis genes were annotated to obtain information on taxonomic identification of the specific chemotactic bacterial species present in the rhizospheres of wild and cultivated rice accessions. More than 60% of the genes that were enriched in the rhizospheres of wild rice accessions were assigned to the genus *Geobacter* (Fig. 6a and Table S5), while the other chemotaxis genes were assigned to seven other bacterial genera, including *Pelobacter*, *Sulfuricella*, *Sulfuricurvum*, *Sulfurospirillum*, *Syntrophus*, *Desulfuromonas* and *Nitrospira* (Fig.6a and Table S5). Among the eight identified genera, only *Nitrospira* was affiliated with the phylum Nitrospirae (Fig. 6a and Table S5), whereas the remaining seven genera were members of the phylum Proteobacteria (Fig. 6a and Table S5). Although the number of enriched chemotaxis genes in the rhizospheres of cultivated rice accessions was less than the number in the rhizospheres of wild rice accessions (Table S2), the identified genes were assigned to a greater number of genera, comprising 13 genera in total. The genera were affiliated with five phyla, including *Blastocatella* from the phylum Acidobacteria, *Desulfobacter* from the phylum Proteobacteria, *Gemmatimonas* from the phylum Gemmatimonadetes, *Ignavibacterium*

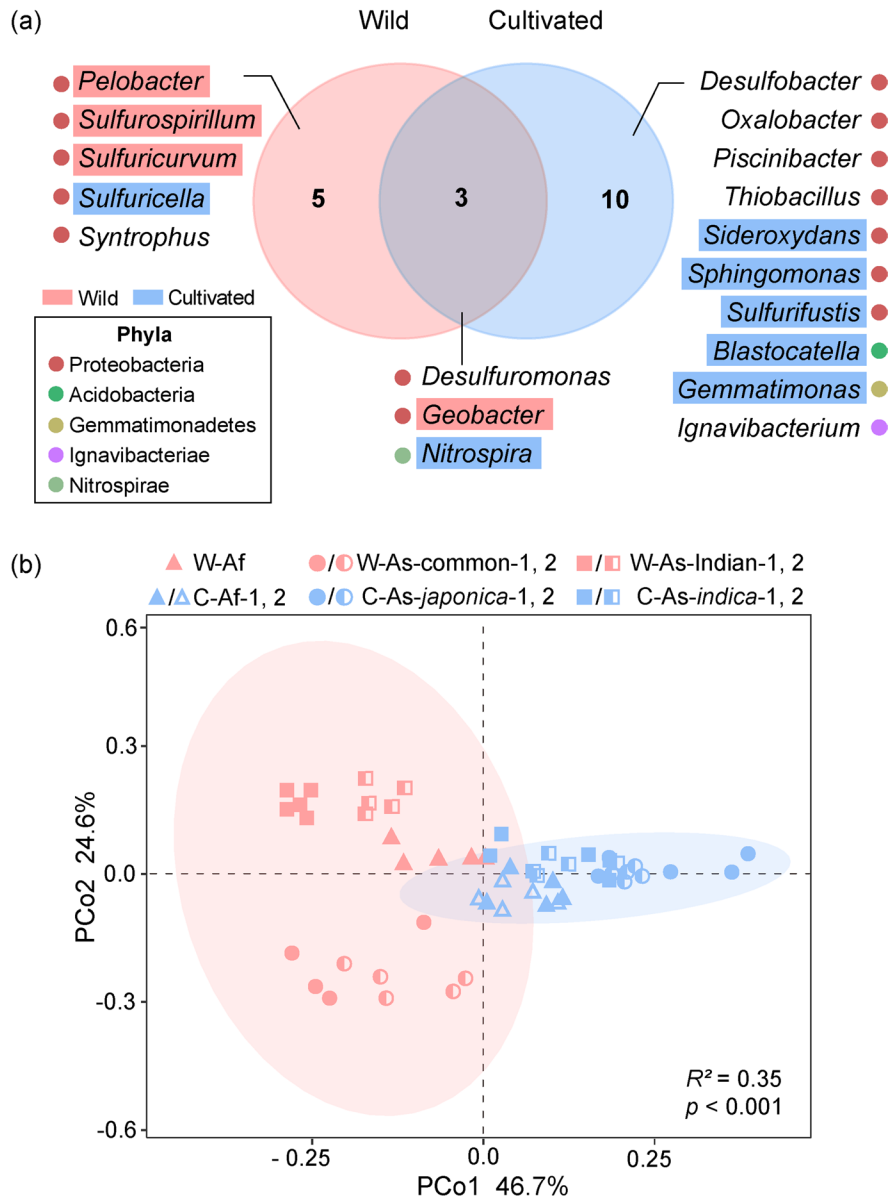

Fig. 6 Venn diagram and PCoA of the core groups of chemotactic bacteria that were predominantly recruited by wild and cultivated rice accessions. (**a**) Venn diagram illustrating the chemotactic bacterial taxa predominantly recruited by wild and cultivated rice. All taxa were identified at the genus level and labeled according to their phyla by different colored circles. Pink and blue rectangles indicate that the genera had a higher relative abundance in the rhizospheres of wild rice and cultivated rice (Student's *t* test, $p < 0.01$), respectively, over the other group. (**b**) PCoA of chemotactic bacterial communities in the rhizospheres of wild and cultivated rice accessions. PCoA was based on Bray-Curtis dissimilarity matrix calculated from the relative abundance of the core groups of chemotactic bacteria. The 95% confidence ellipses were drawn in pink for the wild and in blue for the cultivated rice accessions. Triangles, circles and squares in different colors represent the different wild and cultivated rice accessions. W-Af: African wild rice IRGC 106238; W-As-common-1, 2: common wild rice IRGC 106452 and 106,286; W-As-Indian-1, 2: Indian wild rice IRGC 86655 and 88,949; C-Af-1, 2: African cultivated rice LM8 and WH20; C-As-*japonica*-1, 2: Asian cultivated rice variety *japonica* Jiangxi and Daohuaxiang; C-As-*indica*-1, 2: Asian cultivated rice variety *indica* 106 and Meitezhen

from the Ignavibacteriae, and *Nitrospira* from the phylum Nitrospirae (Fig. 6a and Table S6). Several of the identified highly abundant chemotaxis genes in wild and cultivated rice accessions were assigned to the same genera, including *Geobacter*, *Desulfuromonas* and *Nitrospira* (Fig. 6a and Tables S5-S6). These findings suggest that both wild and cultivated rice can independently recruit in a predominant manner different chemotactic bacteria, although with some overlap as indicated in the Venn diagram (Fig. 6a).

The abundances of the chemotactic bacteria were then analyzed using the results obtained from 16S rRNA gene amplicon sequencing. Among the five genera that were predominantly recruited by wild rice accessions, three had a higher abundance in the rhizospheres of wild rice accessions than in those of cultivated rice accessions (Fig. 6a and Fig. S3). Among the ten genera that were predominantly recruited by cultivated rice accessions, half of them had a higher abundance in the rhizospheres of cultivated rice accessions than in those of wild rice accessions (Fig. 6a and Fig. S3). Among the three genera that were shared by both wild and cultivated rice, *Geobacter* had higher abundance in the rhizospheres of wild rice accessions, whereas *Nitrospira* had higher abundance in the rhizospheres of cultivated rice accessions (Fig. 6a and Fig. S3). PCoA plots of the eighteen bacterial genera also revealed that the compositional profile of the chemotactic bacteria differed between the rhizospheres of wild and cultivated rice accessions (Fig. 6b), suggesting that the core taxa of chemotactic bacteria were differentially recruited by wild and cultivated rice accessions. Clear separations were also observed within the three types of wild rice accessions and within the three types of cultivate rice accessions (Fig. 6b and Table S7), as well as between the two accessions of Indian wild rice (IRGC 86655 and 88,949) and between the two accessions of African cultivated rice (LM8 and WH20) (Fig. 6b and Table S7). These findings suggest that both wild and cultivated rice accessions were able to recruit different taxa of chemotactic bacteria.

The role of the core groups of chemotactic bacteria in the rhizosphere bacterial community were further investigated. Co-occurrence networks of rhizosphere bacterial communities in wild and cultivated rice accessions were constructed by measuring the abundance correlation of pairs of bacteria grouped at the genus level. Results indicated that the co-occurrence network of the rhizosphere bacterial community of wild rice accessions comprised 80 nodes and 139 edges (Fig. 6a and Table S8), while the co-occurrence network of the rhizosphere bacterial community of cultivated rice accessions comprised 47 nodes and 44 edges (Fig. 6b and Table S8). These results suggest that the network in wild rice accessions is more complex than in cultivated rice accessions.

As previously stated, both wild and cultivated rice accessions recruit *Geobacter* (Fig. 6a); however, *Geobacter* was only present in the network of wild rice (Fig. 7a). Notably, only about 25% of the chemotactic bacteria predominantly recruited by wild or cultivated rice accessions were present in the reciprocal network (Figs. 6a and 7a-b), suggesting that not every single genus of chemotactic bacteria provided a significant contribution to community structure. The degree and betweenness centrality of nodes from each network were also analyzed. *Geobacter* was defined as one of the hub taxa in the rhizosphere bacterial community network in wild rice accessions, exhibiting a high degree of and betweenness centrality (Fig. 7c), suggesting that it may play an essential role in structuring the rhizosphere bacterial community of wild rice accessions. None of the three genera (*Blastocatella*, *Desulfobacter* and *Gemmatimonas*) present in the rhizosphere bacterial community network in cultivated rice accessions were identified as hub taxa (Fig. 7d). Based on these results, we conclude that wild and cultivated rice accessions can each recruit specific core groups of chemotactic bacteria, some of which may play a critical role in the associated rhizosphere bacterial communities.

Discussion

Bacterial chemotaxis systems in the rhizospheres of wild and cultivated rice accessions were differentially selected

Chemotaxis, as an important functional trait of bacteria, enables them to respond to and move toward or away from specific chemotactic signals, which may be root exudates or microbial metabolites (Lu et al. 2016; Neal et al. 2012; Tan et al. 2013), thereby mediating plant-microbe and microbe-microbe interactions. The present study revealed that the abundance of chemotaxis genes

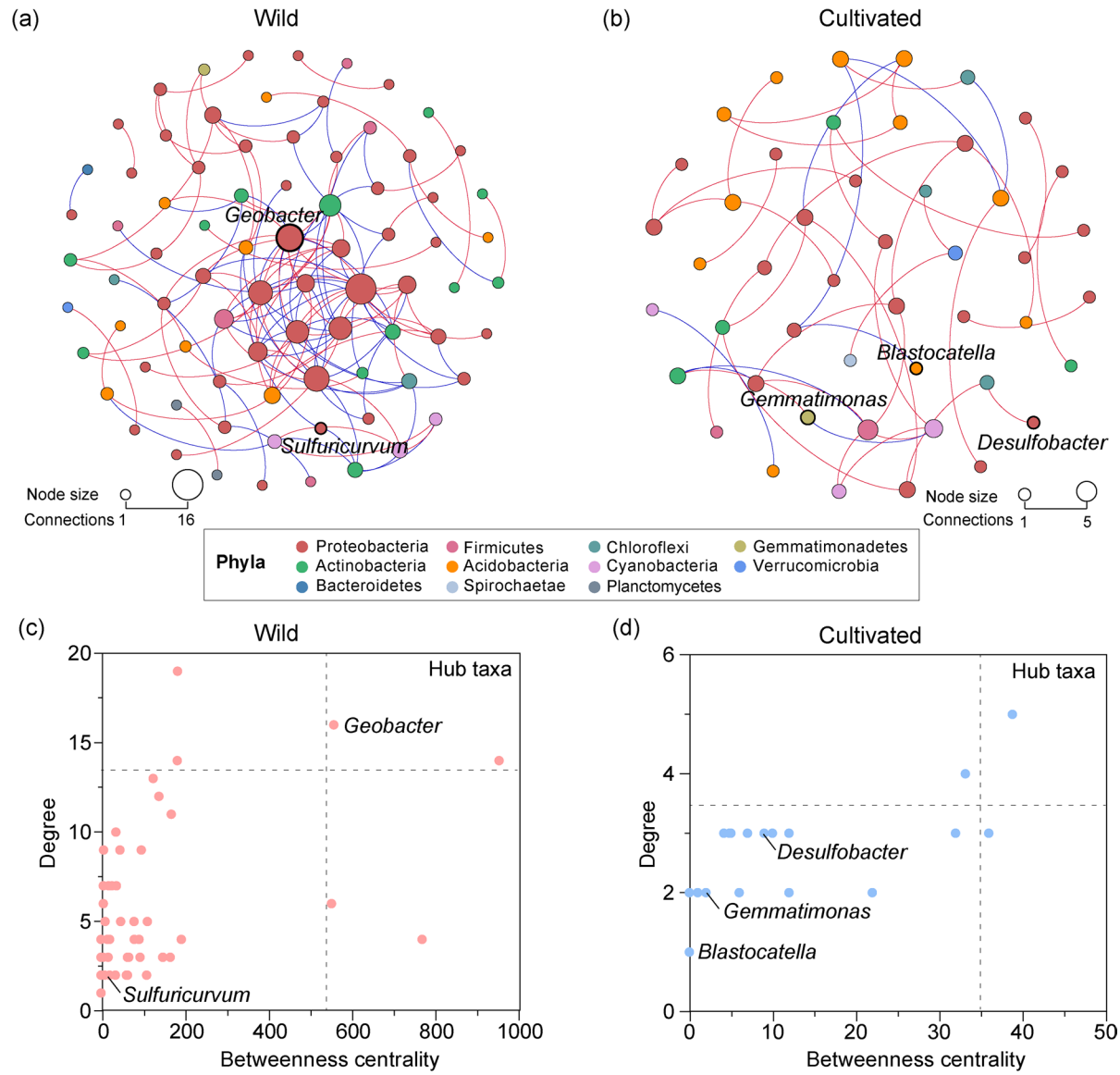

Fig. 7 Co-occurrence analysis of the rhizosphere bacterial communities in wild and cultivated rice accessions. Co-occurrence networks of the rhizosphere bacterial communities of wild (**a**) and cultivated (**b**) rice accessions constructed based on the Spearman's rank correlation analysis. The edges represent significant positive correlations (Spearman's $\rho > 0.8$, $p < 0.01$, red lines) or significant negative correlations (Spearman's $\rho < -0.8$, $p < 0.01$, blue lines). The colored nodes represent taxa identified at the genus level having at least one significant correlation. The size of node is proportional to the number of connections. Each node was colored according to phylum. The distribution of degree and betweenness centrality of nodes (represented by pink and blue circles for wild and cultivated rice accessions, respectively) in the networks of the rhizosphere bacterial communities of wild (**c**) and cultivated (**d**) rice accessions. Nodes showing a high degree and betweenness centrality (the top 2% values, represented by dashed lines) were designated as hub taxa of the rhizosphere bacterial communities of wild and cultivated rice accessions. Nodes representing specific chemotactic bacteria are indicated by their names

was much higher in the rhizospheres of wild rice accessions than it was in cultivated rice accessions. Wild rice generally grows in a harsher environment than cultivated rice, and so the co-evolution of plant host and microbes may result in more adaptive probiotic interactions (Bulgarelli et al. 2013). Thus, the enrichment

of chemotaxis genes in the rhizospheres of wild rice accessions may reflect the types of interactions that occur between wild rice accessions and the soil bacterial community.

Our study also indicated that wild and cultivated rice accessions exerted differential selection pressures on the chemotaxis systems present in the surrounding soil. The distinct compositional profiles of chemotaxis genes may be the consequence of differences in the composition of the rhizosphere bacterial communities of wild and cultivated rice. Notably, accessions of cultivated rice had greater similarity to each other than accessions of wild rice were to each other in regard to the compositional profiles of chemotaxis genes. This suggests that domestication of rice led to a convergence in the composition of chemotaxis systems in the rhizosphere bacterial communities of cultivated rice accessions.

Analysis of the different components of chemotaxis systems indicated that *mcp*, *cheA*, *cheB* and *cheR* had been subjected to a high degree of selection, while other components were not. MCPs, as a component associated with chemotaxis signal processing, detect various chemotaxis signals and regulate the activity of CheA, which is essential for chemotaxis (Tindall et al. 2012). CheB and CheR interact to modulate the signal binding affinity of MCPs, thereby regulating the sensitivity of chemotaxis (Rao et al. 2008). The collective findings of our study suggest that the selection of chemotaxis systems may be driven by changes in chemotactic signals in the rice rhizosphere, such as root exudates (Jin et al. 2019; Scharf et al. 2016).

Root metabolites have driven the selection of bacterial chemotaxis systems in the rhizosphere of rice during domestication

In the present study, wild and cultivated rice exhibited distinctly different root metabolite profiles, and a higher number of metabolites had higher abundance in cultivated rice accessions than wild rice accessions. It may be possible that the roots of cultivated rice are more fragile and more easily broken to liberate intracellular metabolites since it has been reported that domestication might result in changes in root architecture and root exudation (Martínez-Romero et al. 2020). In addition, the wild rice accessions grown under contemporary agricultural soil conditions shall be different from those grown under natural conditions in which wild types and soil microbes co-evolved in their area of origins; and thus, the root exudation of wild rice accessions might also be affected by the changed soil environment. Significant positive correlations were observed between highly abundant metabolites (e.g. malonic acid and L-cysteine from roots of wild and cultivated rice accessions) and the presence of enriched chemotaxis genes (e.g. gene_107266 classified as a K00575 and gene_772 classified as a K03406 in the rhizospheres of wild and cultivated accessions, respectively). Nevertheless, some metabolites, such as fructose, N-methyl-DL-alanine and tartronic acid that exhibited equal levels of abundance in the two rice groups also had high correlations with different chemotaxis genes classified as K03406, K03407, K03412 and K00575 in the rhizospheres of wild and cultivated rice accessions. A possible explanation is that the chemotactic responses of bacteria toward specific metabolites might be affected by the surrounding environment (Bulgarelli et al. 2013), in which root metabolite profiles were distinct and the microbial communities also differed. The metabolites that are differentially abundant between wild and cultivated rice accessions have been reported as having effects on chemotaxis of rhizosphere bacteria. For example, the L-glutamic acid that has higher abundance in cultivated rice was reported to induce chemotactic response of *B. velezensis* SQR9, a plant growth-promoting rhizosphere bacterium (Feng et al. 2019), while another metabolite, L-cysteine, which also has higher abundance in cultivated rice, could induce chemotactic response of *P. fluorescens* Pf0-1, a typical rhizosphere bacterium (Oku et al. 2014). It should be noted that the root metabolites rather than the root exudates were analyzed in this study, and the exact effect of root exudates on the chemotactic responses of specific chemotactic taxa shall be experimentally tested in the future. Based on the differences in correlations between root metabolites and chemotaxis genes in the rhizospheres of wild and cultivated rice accessions, we conclude that the distinct root metabolite profiles, which were affected by domestication, may drive the differential selection of chemotaxis systems by wild and cultivated accessions of rice. Zhalnina et al. (2018) demonstrated that plant root exudate chemistry, together with microbial metabolite substrate preferences, which could be predicted from genome

sequences, drove the assembly of the rhizosphere microbial community, providing strong evidence for the substrate-driven recruitment of microbes. The primary physiological function of chemotaxis is to enable chemotactic bacteria to approach compounds that are of metabolic value (Fernandez et al. 2017). Thus, the relationship between chemotaxis and bacterial substrate preference on shaping bacterial assemblages merits further investigation to determine how the interaction of these components drive bacterial community assembly in the rhizosphere.

The core chemotactic taxa in the rhizosphere bacterial communities of wild and cultivated rice accessions

The differentially abundant chemotaxis genes identified in the rhizospheres of wild and cultivated rice accessions were assigned to chemotactic bacteria affiliated with five major phyla, namely Proteobacteria, Acidobacteria, Gemmatimonadetes, Ignavibacteriae and Nitrospirae, which represent the dominant taxa found in the plant rhizosphere (Bulgarelli et al. 2012; Edwards et al. 2015; Xu et al. 2018). These findings showed that the well-known chemotactic bacteria are widely distributed in the rhizospheres of the investigated wild and cultivated rice accessions. Consistent with our findings, Buchan et al. (2010) reported that *cheA* genes in the rhizospheres of wheat and cowpea were also affiliated with several phyla, including Proteobacteria, Acidobacteria, Gemmatimonadetes and Nitrospirae. Notably, fewer chemotaxis genes (23 in total) were assigned to more bacterial genera (13 in total) in the rhizospheres of cultivated rice accessions than in wild rice accessions (31 genes and 8 genera). These data indicate that many chemotactic bacteria share orthologous chemotaxis genes in the rhizospheres of cultivated rice accessions, which also suggests that rice domestication has led to a reduction in the functional specificity of chemotaxis systems.

Co-occurrence analysis has been widely used to explore the networks of microbial communities and reveal patterns of ecological interactions (Fan et al. 2018; Ma et al. 2016). In the present study, we identified striking differences in the network structure of the rhizosphere microbial communities of wild and cultivated rice. Notably, wild rice had a more complex and highly connected community than cultivated rice. The abundance of chemotaxis genes was also higher in the rhizosphere of wild rice than in cultivated rice. Consistent with these results, Mendes et al. (2018) reported that a common bean (*Phaseolus vulgaris*) cultivar resistant to the fungal root pathogen *Fusarium oxysporum* had a more complex rhizosphere community and a higher abundance of chemotaxis genes compared with a common bean cultivar that was susceptible to the same pathogen. The positive correlation between chemotaxis gene abundance and bacterial community complexity supports the premise that chemotaxis is involved in the assembly of the rhizosphere bacterial community. Co-occurrence network analysis can also help identify potential hub taxa that are crucial to the interaction patterns. In this regard, Agler et al. (2016) found that abiotic factors and host genotype may act directly on hub taxa, which could transmit the impact to the larger microbial community via microbe-microbe interactions; thus demonstrating the vital role that hub taxa play in community assembly. In our study, the chemotactic genus *Geobacter*, an important dissimilatory Fe (III) reducer that is commonly found in rice paddy fields (Li et al. 2020b), was identified as one of the hub taxa in the rhizosphere bacterial community of wild rice accessions. The genomes of several species of *Geobacter* have been analyzed and revealed a large number of chemotaxis genes and a diverse set of MCPs with different sensing domains (Tran et al. 2008). As chemotaxis has been shown to be one of the mechanisms that mediate microbe-microbe interactions (Garbeva and de Boer 2009; Lu et al. 2016), chemotaxis may be used by *Geobacter* to interact with other bacteria to structure the rhizosphere bacterial community of wild rice accessions. In contrast, however, *Geobacter* was not even present in the network in the rhizosphere bacterial community of cultivated rice accessions, where a distinct change in network occurred relative to wild rice. The chemotactic bacteria present in the rhizosphere network of cultivated rice, including *Blastocatella*, *Gemmatimonas* and *Desulfobacter*, were shown to be less connected to other bacteria. These findings suggest that domestication might also have shifted the interaction profile of bacteria in the rhizospheres of cultivated rice accessions. As mentioned above, the wild rice accessions were grown under contemporary agricultural soil conditions rather than the original soil where wild rice accessions co-evolved with microbes, and this may also affect the assembly and interaction networks of bacterial community.

In conclusion, results of the present study indicated that the selection of chemotaxis systems in the rhizospheres of cultivated rice accessions was distinctly different from that of wild rice and may be driven by

the changes in the root metabolite profile that was affected by domestication. The results emphasize the importance of chemotaxis in the complex processes of microbial community assemblage associated with rice domestication, and provide a potential target for restructuring the rhizomicrobiome in support of the development of climate-smart agricultural production systems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-021-05036-2.

Authors' contributions CT conceived and designed the study; JZ and WL helped with the experiment design; HX, YC and DC carried out the experiments; LT and SS collected the samples; YS, LT and JC analyzed the data and prepared figures and tables with the input of WL and L-SPT; YS, WL, L-SPT and CT wrote the manuscript. EEK and JAvV helped with the improvement of the manuscript. All authors read and approved the final manuscript.

Funding This work was supported by the National Natural Science Foundation of China (41920104008, 42007034), the National Key Research and Development Program of China (2016YFC0501202), the Science Foundation of Chinese Academy of Sciences (XDA23070501), the Cooperative Project between CAS and Jilin Province of China (2019SYHZ0039) and the Science and Technology Development Project of Jilin Province of China (20190303070SF, 20200501003GX, YDZJ202101ZYTS006). Publication number 7205 of the Netherlands Institute of Ecology (NIOO-KANW).

Data availability Shotgun metagenomic sequencing and 16S rRNA gene amplicon sequencing data are available on NCBI under the Bioproject accession number PRJNA632564 and PRJNA639671, respectively.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Agler MT, Ruhe J, Kroll S, Morhenn C, Kim ST, Weigel D, Kemen EM (2016) Microbial hub taxa link host and abiotic factors to plant microbiome variation. PLoS Biol 14:e1002352. https://doi.org/10.1371/journal.pbio.1002352

Badri DV, Chaparro JM, Zhang R, Shen Q, Vivanco JM (2013) Application of natural blends of phytochemicals derived from the root exudates of *Arabidopsis* to the soil reveal that phenolic-related compounds predominantly modulate the soil microbiome. J Biol Chem 288:4502–4512. https://doi.org/10.1074/jbc.M112.433300

Bastian M, Heymann S, Jacomy M (2009) Gephi: an open source software for exploring and manipulating networks. ICWSM

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B 57:289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Berendsen RL, Vismans G, Yu K, Song Y, de Jonge R, Burgman WP, Burmolle M, Herschend J, Bakker P, Pieterse CMJ (2018) Disease-induced assemblage of a plant-beneficial bacterial consortium. ISME J 12:1496–1507. https://doi.org/10.1038/s41396-018-0093-1

Bolger AM, Lohse M, Usadel B (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30:2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Buchan A, Crombie B, Alexandre GM (2010) Temporal dynamics and genetic diversity of chemotactic-competent microbial populations in the rhizosphere. Environ Microbiol 12:3171–3184. https://doi.org/10.1111/j.1462-2920.2010.02290.x

Bulgarelli D, Rott M, Schlaeppi K, Ver Loren van Themaat E, Ahmadinejad N, Assenza F, Rauf P, Huettel B, Reinhardt R, Schmelzer E, Peplies J, Gloeckner FO, Amann R, Eickhorst T, Schulze-Lefert P (2012) Revealing structure and assembly cues for *Arabidopsis* root-inhabiting bacterial microbiota. Nature 488:91–95. https://doi.org/10.1038/nature11336

Bulgarelli D, Schlaeppi K, Spaepen S, Ver Loren van Themaat E, Schulze-Lefert P (2013) Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol 64:807–838. https://doi.org/10.1146/annurev-arplant-050312-120106

Chang J, Sun Y, Tian L, Ji L, Luo S, Nasir F, Kuramae EE, Tian CJ (2021) The structure of rhizosphere fungal communities of wild and domesticated rice: changes in diversity and co-occurrence patterns. Front Microbiol 12:610823. https://doi.org/10.3389/fmicb.2021.610823

Choi JY, Platts AE, Fuller DQ, Hsing YI, Wing RA, Purugganan MD (2017) The rice paradox: multiple origins but single domestication in Asian rice. Mol Biol Evol 34:969–979. https://doi.org/10.1093/molbev/msx049

Cooper JE (2007) Early interactions between legumes and rhizobia: disclosing complexity in a molecular dialogue. J Appl Microbiol 103:1355–1365. https://doi.org/10.1111/j.1365-2672.2007.03366.x

Edgar RC (2013) UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat Methods 10:996–998. https://doi.org/10.1038/nmeth.2604

Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R (2011) UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27:2194–2200. https://doi.org/10.1093/bioinformatics/btr381

Edwards J, Johnson C, Santos-Medellin C, Lurie E, Podishetty NK, Bhatnagar S, Eisen JA, Sundaresan V (2015) Structure, variation, and assembly of the root-associated microbiomes of rice. Proc Natl Acad Sci U S A 112:e911–e920. https://doi.org/10.1073/pnas.1414592112

Fan K, Weisenhorn P, Gilbert JA, Chu H (2018) Wheat rhizosphere harbors a less complex and more stable microbial co-occurrence pattern than bulk soil. Soil Biol Biochem 125:251–260. https://doi.org/10.1016/j.soilbio.2018.07.022

Feng H, Zhang N, Fu R, Liu Y, Krell T, Du W, Shao J, Shen Q, Zhang R (2019) Recognition of dominant attractants by key chemoreceptors mediates recruitment of plant growth-promoting rhizobacteria. Environ Microbiol 21:402–415. https://doi.org/10.1111/1462-2920.14472

Fernandez M, Matilla MA, Ortega A, Krell T (2017) Metabolic value chemoattractants are preferentially recognized at broad ligand range chemoreceptor of *Pseudomonas putida* KT2440. Front Microbiol 8:990. https://doi.org/10.3389/fmicb.2017.00990

Garbeva P, de Boer W (2009) Inter-specific interactions between carbon-limited soil bacteria affect behavior and gene expression. Microb Ecol 58:36–46. https://doi.org/10.1007/s00248-009-9502-3

Hasegawa T, Kato Y, Okabe A, Itoi C, Ooshiro A, Kawaide H, Natsume M (2019) Effect of secondary metabolites of tomato (*Solanum lycopersicum*) on chemotaxis of *Ralstonia solanacearum*, pathogen of bacterial wilt disease. J Agric Food Chem 67:1807–1813. https://doi.org/10.1021/acs.jafc.8b06245

Hu L, Robert CAM, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, van der Heijden MGA, Schlaeppi K, Erb M (2018) Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat Commun 9:2738. https://doi.org/10.1038/s41467-018-05122-7

Jacoby R, Peukert M, Succurro A, Koprivova A, Kopriva S (2017) The role of soil microorganisms in plant mineral nutrition-current knowledge and future directions. Front Plant Sci 8:1617. https://doi.org/10.3389/fpls.2017.01617

Jin Y, Zhu H, Luo S, Yang W, Zhang L, Li S, Jin Q, Cao Q, Sun S, Xiao M (2019) Role of maize root exudates in promotion of colonization of *Bacillus velezensis* strain S3-1 in rhizosphere soil and root tissue. Curr Microbiol 76:855–862. https://doi.org/10.1007/s00284-019-01699-4

Khush GS (2005) What it will take to feed 5.0 billion rice consumers in 2030. Plant Mol Biol 59:1–6. https://doi.org/10.1007/s11103-005-2159-5

Kim H, Lee KK, Jeon J, Harris WA, Lee YH (2020) Domestication of *Oryza* species eco-evolutionarily shapes bacterial and fungal communities in rice seed. Microbiome 8:20. https://doi.org/10.1186/s40168-020-00805-0

Kovach MJ, Sweeney MT, McCouch SR (2007) New insights into the history of rice domestication. Trends Genet 23:578–587. https://doi.org/10.1016/j.tig.2007.08.012

Kwak MJ, Kong HG, Choi K, Kwon SK, Song JY, Lee J, Lee PA, Choi SY, Seo M, Lee HJ, Jung EJ, Park H, Roy N, Kim H, Lee MM, Rubin EM, Lee SW, Kim JF (2018) Rhizosphere microbiome structure alters to enable wilt resistance in tomato. Nat Biotechnol 36:1100–1109. https://doi.org/10.1038/nbt.4232

Li W, Zhang Y, Li H, Zhang C, Zhang J, Uddin J, Liu X (2020a) Effect of soybean oligopeptide on the growth and metabolism of *Lactobacillus acidophilus* JCM 1132. RSC Adv 10:16737–16748. https://doi.org/10.1039/d0ra01632b

Li X, Ding L, Li X, Zhu Y (2020b) Abundance, diversity, and structure of Geobacteraceae community in paddy soil under long-term fertilization practices. Appl Soil Ecol 153:103577. https://doi.org/10.1016/j.apsoil.2020.103577

Lisec J, Schauer N, Kopka J, Willmitzer L, Fernie AR (2006) Gas chromatography mass spectrometry-based metabolite profiling in plants. Nat Protoc 1:387–396. https://doi.org/10.1038/nprot.2006.59

Lu H, Chen J, Jia Y, Cai M, Lee PKH (2016) Transcriptomic responses of the interactions between *Clostridium cellulovorans* 743B and *Rhodopseudomonas palustris* CGA009 in a cellulose-grown coculture for enhanced hydrogen production. Appl Environ Microbiol 82:4546–4559. https://doi.org/10.1128/AEM.00789-16

Ma B, Wang H, Dsouza M, Lou J, He Y, Dai Z, Brookes PC, Xu J, Gilbert JA (2016) Geographic patterns of co-occurrence network topological features for soil microbiota at continental scale in eastern China. ISME J 10:1891–1901. https://doi.org/10.1038/ismej.2015.261

Magoc T, Salzberg SL (2011) FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics 27:2957–2963. https://doi.org/10.1093/bioinformatics/btr507

Martínez-Romero E, Aguirre-Noyola JL, Taco-Taype N, Julio M-R, Zuniga-Dávila D (2020) Plant microbiota modified by plant domestication. Syst Appl Microbiol 43:126106. https://doi.org/10.1016/j.syapm.2020.126106

Mendes LW, Raaijmakers JM, de Hollander M, Mendes R, Tsai SM (2018) Influence of resistance breeding in common bean on rhizosphere microbiome composition and function. ISME J 12:212–224. https://doi.org/10.1038/ismej.2017.158

Moriya Y, Itoh M, Okuda S, Yoshizawa AC, Kanehisa M (2007) KAAS: an automatic genome annotation and pathway reconstruction server. Nucleic Acids Res 35:W182–W185. https://doi.org/10.1093/nar/gkm321

Mostofa MG, Li W, Nguyen KH, Fujita M, Tran LP (2018) Strigolactones in plant adaptation to abiotic stresses: an emerging avenue of plant research. Plant Cell Environ 41:2227–2243. https://doi.org/10.1111/pce.13364

Neal AL, Ahmad S, Gordon-Weeks R, Ton J (2012) Benzoxazinoids in root exudates of maize attract *Pseudomonas putida* to the rhizosphere. PLoS One 7:e35498. https://doi.org/10.1371/journal.pone.0035498

Oku S, Komatsu A, Nakashimada Y, Tajima T, Kato J (2014) Identification of *Pseudomonas fluorescens* chemotaxis sensory proteins for malate, succinate, and fumarate, and their involvement in root colonization. Microbes Environ 29:413–419. https://doi.org/10.1264/jsme2.ME14128

Parkinson JS, Hazelbauer GL, Falke JJ (2015) Signaling and sensory adaptation in *Escherichia coli* chemoreceptors: 2015 update. Trends Microbiol 23:257–266. https://doi.org/10.1016/j.tim.2015.03.003

Parks DH, Tyson GW, Hugenholtz P, Beiko RG (2014) STAMP: statistical analysis of taxonomic and functional profiles. Bioinformatics 30:3123–3124. https://doi.org/10.1093/bioinformatics/btu494

Perez-Jaramillo JE, Mendes R, Raaijmakers JM (2016) Impact of plant domestication on rhizosphere microbiome assembly and functions. Plant Mol Biol 90:635–644. https://doi.org/10.1007/s11103-015-0337-7

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799. https://doi.org/10.1038/nrmicro3109

Raina JB, Fernandez V, Lambert B, Stocker R, Seymour JR (2019) The role of microbial motility and chemotaxis in symbiosis. Nat Rev Microbiol 17:284–294. https://doi.org/10.1038/s41579-019-0182-9

Rao CV, Glekas GD, Ordal GW (2008) The three adaptation systems of *Bacillus subtilis* chemotaxis. Trends Microbiol 16:480–487. https://doi.org/10.1016/j.tim.2008.07.003

Scharf BE, Hynes MF, Alexandre GM (2016) Chemotaxis signaling systems in model beneficial plant-bacteria associations. Plant Mol Biol 90:549–559. https://doi.org/10.1007/s11103-016-0432-4

Shenton M, Iwamoto C, Kurata N, Ikeo K (2016) Effect of wild and cultivated rice genotypes on rhizosphere bacterial community composition. Rice (N Y) 9:42. https://doi.org/10.1186/s12284-016-0111-8

Tan S, Yang C, Mei X, Shen S, Raza W, Shen Q, Xu Y (2013) The effect of organic acids from tomato root exudates on rhizosphere colonization of *Bacillus amyloliquefaciens* T-5. Appl Soil Ecol 64:15–22. https://doi.org/10.1016/j.apsoil.2012.10.011

Tindall MJ, Gaffney EA, Maini PK, Armitage JP (2012) Theoretical insights into bacterial chemotaxis. Wiley Interdisciplinary Reviews-Systems Biology and Medicine 4:247–259. https://doi.org/10.1002/wsbm.1168

Tran HT, Krushkal J, Antommattei FM, Lovley DR, Weis RM (2008) Comparative genomics of Geobacter chemotaxis genes reveals diverse signaling function. BMC Genomics 9:471. https://doi.org/10.1186/1471-2164-9-471

Wang M, Yu Y, Haberer G, Marri PR, Fan C, Goicoechea JL, Zuccolo A, Song X, Kudrna D, Ammiraju JS, Cossu RM, Maldonado C, Chen J, Lee S, Sisneros N, de Baynast K, Golser W, Wissotski M, Kim W, Sanchez P, Ndjiondjop MN, Sanni K, Long M, Carney J, Panaud O, Wicker T, Machado CA, Chen M, Mayer KF, Rounsley S, Wing RA (2014) The genome sequence of African rice (*Oryza glaberrima*) and evidence for independent domestication. Nat Genet 46:982–988. https://doi.org/10.1038/ng.3044

Wuichet K, Zhulin IB (2010) Origins and diversification of a complex signal transduction system in prokaryotes. Sci Signal 3:ra50. https://doi.org/10.1126/scisignal.2000724

Xu J, Zhang Y, Zhang P, Trivedi P, Riera N, Wang Y, Liu X, Fan G, Tang J, Coletta-Filho HD, Cubero J, Deng X, Ancona V, Lu Z, Zhong B, Roper MC, Capote N, Catara V, Pietersen G, Verniere C, Al-Sadi AM, Li L, Yang F, Xu X, Wang J, Yang H, Jin T, Wang N (2018) The structure and function of the global citrus rhizosphere microbiome. Nat Commun 9:4894. https://doi.org/10.1038/s41467-018-07343-2

Zhalnina K, Louie KB, Hao Z, Mansoori N, da Rocha UN, Shi S, Cho H, Karaoz U, Loque D, Bowen BP, Firestone MK, Northen TR, Brodie EL (2018) Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nat Microbiol 3:470–480. https://doi.org/10.1038/s41564-018-0129-3