Environ Sci Pollut Res (2017) 24:16458–16464
DOI 10.1007/s11356-017-9254-4

RESEARCH ARTICLE

Endophytic bacterial and fungal communities transmitted from cotyledons and germs in peanut (*Arachis hypogaea* L.) sprouts

Yali Huang[1] · Zaoyuan Kuang[1] · Zujun Deng[2] · Ren Zhang[1] · Lixiang Cao[3]

Received: 10 October 2016 / Accepted: 10 May 2017 / Published online: 27 May 2017

Abstract Seed-borne endophytes could be transmitted into sprouts. Whether this happened in peanuts and the difference between microbial taxa in peanut germs and cotyledons remain unknown. In this research, Illumina-based sequencing was employed to investigate the microbial taxa in peanut germs, cotyledons, and sprouts. Sulfur-oxidizing bacteria was isolated and inoculated into peanut sprouts, and then, the growth of peanut seedlings was measured. The results illustrated that diverse bacteria and fungi were detected in peanut germs, cotyledons, and sprouts. The number of bacterial OTUs declined with the germination from germs and cotyledons to sprouts. However, the number of fungal OTUs increased during the seedling procedure. Seed-borne dominant bacterial genera *Halothiobacillus* and *Synechococcus* and fungal genera *Humicola*, *Emericella*, and *Penicillium* were detected in sprouts. Based on the endophytic community information, the *Halothiobacillus* strains were isolated from sprouts. Pot experiments that illustrated the growth of peanut seedlings inoculated with the strain were promoted. These results provide new understanding into plant-microbe interactions in peanut and suggest that the selection for biocontrol agents based on mycobiome and bacteriome analysis is reliable and feasible compared with the present greenhouse selection.

Keywords Endophyte · *Halothiobacillus* · *Humicola* · Peanut · Plant microbiome · Sulfur-oxidizing bacteria

Responsible editor: Philippe Garrigues

✉ Ren Zhang
5686522@qq.com

✉ Lixiang Cao
lssclx@163.com

[1] College of Fundamental Medical Sciences, Guangzhou University of Chinese Medicine, Guangzhou, China

[2] School of Basic Courses, Guangdong Provincial Key Laboratory of Pharmaceutical Bioactive Substances, Guangdong Pharmaceutical University, Guangzhou, China

[3] School of Life Sciences, Sun Yat-sen University, Guangzhou, China

Introduction

Peanut (*Arachis hypogaea* L.) is a vital oilseed crop. Oil extracted from peanut seeds is an important constituent of food oil supply in China. Endophytic and epiphytic microbiota, such as commensal, synergistic, and potentially pathogenic microbes, is present in crop seeds (Nicolaisen et al. 2014), which is related to seed storage, plant growth, and development (Links et al. 2014). Evidence presented that *Aspergillus* sp. producing carcinogenic mycotoxins was identified in peanut as symptomless endophytes, which suggests the potential for concern as pathogens and as food safety hazard (Palencia et al. 2010). However, further research suggested that mature peanut seeds from the experimental and control plants contained several species of nonpathogenic endophytic bacteria, and the *Bacillus* species in seeds demonstrated activity against *Aspergillus flavus* (Sobolev et al. 2013). So, the correlation between bacteria and fungi in peanut seeds should be further studied.

The peanut plant accommodates only selected bacterial species from diverse soil populations (Sobolev et al. 2013). Seed bacterization with phylloplane isolates promoted peanut growth indicating the possibility of isolating beneficial rhizosphere bacteria from different habitats (Kishore et al. 2005). The selected bacteria could potentially be utilized for the biocontrol of toxicogenic fungi (Wang et al. 2012). So, beneficial endophytic microbes promote peanut growth and control

toxicogenic fungi could be isolated from soils (Ibañez et al. 2009, 2014; Taurian et al. 2010; Fabra et al. 2010). Agricultural environment may provide a way to reduce the toxigenic fungal contamination and mycotoxins in peanuts (Goncalez et al. 2008). However, the predominance of *Aspergillus* in hulls and kernels has been identified and 93.8% of *A. flavus* strains were producers of aflatoxin B1 and B2 (Nakai et al. 2008). Aflatoxin is commonly found presenting deeply in individual kernels and the aflatoxin contents of different portions of peanut kernels have been determined (Goldblatt 1971). So, the endophytic microbiota transmitted from seeds to seedlings would be helpful for control toxicogenic fungi and reduce the mycotoxin contents.

During seed germination, external environmental conditions affect dormant seeds and initiate dormancy-breaking signals. As seeds set out to germinate, seedling microbial communities begin to form gradually based on seed endophytes (Johnston-Monje and Raizada 2011). The transmission can choose beneficial endosymbionts, exclude pathogenic microbes, and benefit host plants by delivering beneficial endosymbionts to the next generation (Truyens et al. 2015). The peanut seeds consisted of germs and cotyledons; however, the difference of bacterial and fungal flora between peanut germs and cotyledons is unknown. Whether the flora in sprouts is derived from germs or cotyledons is still unknown. Next-generation sequencing is a robust approach that could be employed to decipher microbiome of plants, and the microorganisms that identified by microbiome analysis could be exploited to enhance host plant health and production (Mendes et al. 2013).

Herein, our objective was to identify the endophyte taxa of peanut seeds that can be transmitted to sprouts and their effects on sprout growth. Specifically, we isolated total DNA from seed germs, cotyledons, and sprouts of peanuts, and employed Illumina-based sequencing to analyze the conserved genomic regions of bacteria and fungi. Then, we compared the bacterial and fungal communities, identified the transmitted microbial taxa from seeds, and analyzed their effects on sprouts.

Material and methods

Seed germination

To surface disinfection, the peanut (*Arachis hypogaea* L., $n = 5$) seeds were immersed in 75% (*v*/*v*) ethanol for 5 min, sodium hypochlorite solution containing 5% active chlorine for 5 min, and then were rinsed with sterile distilled water for three times. The surface-disinfected seeds were germinated on sterilized moistened filer paper (Xinhua, Hangzhou, China) at 25 °C. Four days later, the genomic DNA was isolated from the processed sprouts. The surface-disinfected seed without germination were divided into germ and cotyledon parts for DNA isolation. The assay of each group (sprout, germ, and cotyledon) of samples was repeated three times.

DNA extraction

The genomic DNA was isolated from the peanut seed germs (designated as Pgerm), cotyledons (designated as Pcotyledon), and sprouts (designated as Psprout) with E.Z.N.A. HP Plant Miniprep DNA Kit (Omega Bio-Tek). The quality of genomic DNA was analyzed by 1% agarose gel electrophoresis.

Conservative region amplification and Illumina MiSeq sequencing

The 16S ribosomal RNA (rRNA) gene fragments and the ITS1 regions of fungal rRNA gene were amplified and amplicons were sequenced according to the procedure (Huang et al. 2016). Briefly, the triplicate PCR reactions for each sample were combined into a single volume and then purified using GeneJET Gel Extraction Kit (Thermo Scientific). The sequencing libraries were constructed according to the standard protocol for NEB Next® Ultra™ DNA Library Prep Kit (New England Biolabs). Sequencing was carried by Guangzhou Magigen Biotechnology Co., Ltd.

Data preprocessing and diversity analyses

Sequence processing, analysis, and community comparisons were performed as previously described (Huang et al. 2016). The sequencing data can be available in the NCBI Sequence Read Archive (SRA) database given the accession number SRP055979.

Isolation of *Halothiobacillus* from sprouts

The peanut sprouts under aseptic conditions were clip into about 0.2 × 0.2 cm pieces. Then, the pieces were put into mineral medium (MM) (Park et al. 2008) and incubated at 28 °C (Shi et al. 2011). Colonies formed on plates were transferred on mineral medium with 2 M NaCl (selective medium for *Halothiobacillus*) to obtain the pure culture (Sorokin et al. 2006).

Pot experiments

Soil with texture of sandy loam, which contains 70% sand, 15% silt, and 15% clay, was obtained from the suburbs of Guangzhou, China. The bacterial strains grown in MM medium were harvested by centrifugation, washed twice, and suspended in saline (0.85% NaCl) solution. Meanwhile, the peanut seeds were sterilized in NaClO solution, which contains 6.5% active chlorine, for 30 min and rinsed three times

with sterile distilled water. The seeds were inoculated by soaking in bacterial suspension of 10^7 cfu ml^{-1} for 2 h. The seeds soaked in sterile water were used as a negative control. All seeds were sowed in the test soils amended with sulfur (50 mg kg^{-1} of soil). Ten seeds were sowed in each pot and each treatment contained three pots. The soil moisture was maintained at the saturated condition. The plants were grown at 25 °C and a 16/8 h day/night regime in a glasshouse. The shoot length (cm), shoot fresh weight (g), and root fresh weight (g) were evaluated 28 days after germination (Anandham et al. 2014). Each treatment contains three pots of seedlings.

Statistical analysis

For unweighted and weighted Unifrac distances were calculated by QIIME (V1.7.0) (Kõljalg et al. 2013). KRONA was used to visualize the phylogenetic relationship of different microbial taxa (Ondov et al. 2011). Estimates of species richness and relative diversity level were provided by Shannon, Simpson, Chao1, ACE, and coverage indices (Kemp and Aller 2004). Statistical analysis was performed by previous methods (Huang et al. 2016).

Results

Overview of fungal and bacterial community diversity

After low quality, chimeric reads were filtered out, 260,308 bacterial sequences were generated with an average length of 406 bp, and 183,204 fungal sequences were generated with an average length of 272 bp (Table 1). Based on their shared sequence similarity at a 97% threshold, sequences of each sample were clustered into an average of 66 bacterial OTUs ranging from 29 to 102 OTUs, and an average of 26 fungal OTUs ranging from 18 to 31 OTUs with coverage more than 0.99. The alpha diversity indices indicated that the more diverse bacterial OTUs were detected in the germs and cotyledons than those in sprouts; nevertheless, the sprouts contain similar diverse fungi with germs and cotyledons (Table 2).

Although the germs and cotyledons were divided from surface sterilized seeds, and the sprouts are segregated from environmental bacteria and fungi during germination, diverse endophytes in these samples were detected. A total of 102 bacterial OTUs were obtained in cotyledons and 29 OTUs in germs, and 4 bacterial OTUs coexisted in germs and cotyledons simultaneously. With the germination, 14 bacterial OTUs of cotyledons were still found in sprouts, and 6 OTUs of germs were found in sprouts. Moreover, 4 OTUs were found in germs, cotyledons, and sprouts simultaneously (Fig. 1). Unlike endophytic bacteria, the sprouts and germs contained more fungal OTU than cotyledons, and 20 OTUs were found in germs and sprouts simultaneously; 17 OTUs of cotyledons were still detected in sprouts (Fig. 2), and 15 OTUs were detected in sprouts, germs, and cotyledons simultaneously.

The community structure and composition of fungi and bacteria

Representative bacterial sequences of each OTU were assigned into the domains *Bacteria* (99.99% of the total data set), of which *Halothiobacillus* dominated the overall bacterial genera (31.0%) (Fig. 3). The *Synechococcus* were the second most dominant (5.2%). Representative fungal sequences of each OTU were assigned into the domains *Fungi* (100% of the total data set), of which the *Rhizopus* dominated the overall fungal genera (0.4%) (Fig. 4). *Penicillium* was the second most dominant (0.1%). The dominant fungal and bacterial taxa in three peanut samples were different from each other. *Halothiobacillus*, *Synechococcus*, *Paracoccus*, *Agrobacterium*, and *Gallionella* were the most abundant bacterial genera in cotyledons. The dominant bacteria in germs were *Synechococcus*, *Halothiobacillus*, *Mycobacterium*, and *Rhodococcus* among all the bacterial genera. *Halothiobacillus*, *Synechococcus*, *Burkholderia*, and *Paracoccus* were found to be the most abundant bacterial genera in sprouts. With the germination, the dominant bacterial genera *Halothiobacillus* and *Synechococcus* were still the most detected genera in spouts. Other bacterial genera *Erwinia*, *Hyphomonas*, and *Devosia* were detected in cotyledons and sprouts simultaneously.

For the dominant fungal genera in the peanut plants, *Rhizopus*, *Emericella*, and *Penicillium* were found the most in all samples (Fig. 4). *Humicola*, *Emericella*, and *Penicillium* were the dominant fungal genera in germs, and cotyledons

Table 1 Summary of the features of valid tags of the samples of cotyledons (Pcotyledon), germs (Pgerm) of peanut seeds, and peanut sprouts (Psprout)

Samples	V3–V4 tags				ITS1 tags			
	Numbers	Total length (bp)	Max length (bp)	Min length(bp)	Numbers	Total length (bp)	Max length (bp)	Min length (bp)
Pcotyledon	94,102	38,211,779	432	368	56,393	15,341,027	287	217
Pgerm	96,236	39,071,113	430	350	58,670	15,945,686	328	205
Psprout	69,970	28,410,391	430	368	68,141	18,515,388	366	206

Table 2 Summary of species richness estimators of the samples of cotyledons (Pcotyledon), germs (Pgerm) of peanut seeds, and peanut sprouts (Psprout)

Samples	Bacterial OTUs					Fungal OTUs				
	Chao1	ACE	Shannon	Simpson	Coverage	Chao1	ACE	Shannon	Simpson	Coverage
Pcotyledon	2323.5	1997.3	1.04	0.36	0.996	18.8	20.6	0.38	0.11	0.999
Pgerm	1820.6	1829.6	1.03	0.36	0.996	31.0	31.6	0.43	0.12	0.999
Psprout	1232.2	1416.4	0.91	0.31	0.996	30.3	30.9	0.49	0.13	0.999

contained *Emericella* as the dominant genus. The dominant fungal genera of germs, such as *Humicola*, *Emericella*, and *Penicillium*, were still detected in sprouts. With the germination, the sprouts obtained the *Rhizopus* as dominant fungal genera. The *Emericella* was detected in sprouts, germs, and cotyledons, simultaneously, whereas the *Emericella* detected in cotyledons were at low abundance.

Pot experiments

A pure culture of *Halothiobacillus* was obtained and designated as SOB4. The pot experiments demonstrated the stimulation effects of sulfur oxidation bacteria strain SOB4 in peanut sprouts. Compared with the negative controls, the growth of peanut seedlings inoculated with strain SOB4 was facilitated ($P < 0.05$). Root fresh weight, shoot length, and shoot fresh weight were promoted by 73, 35, and 84%, respectively (Table 3).

Discussion

Peanut is a widespread leguminous plant of great agricultural and economic significance, and nodulation by native bacteria is usually assumed to be adequate (Taurian et al. 2010; Angelini et al. 2011). The rhizosphere and endophytic bacteria that enhanced plant yield had been isolated and detected in the previous studies (Ibañez et al. 2009; Haldar et al. 2011). However, the bacterial flora transmitted from peanut seed was not reported. Our results suggested that the more diverse bacteria were detected in germs and cotyledons than those in sprouts; nevertheless, the sprouts contain more diverse fungi than germs and cotyledons. The seed's physiological state might influence the microbial community during the germination process. In the study, the surface-disinfected seeds were germinated on sterilized moistened filter paper, the sprouts did not obtain bacteria and fungi from environments, and the assorted bacteria and fungi in sprouts might come from germs and cotyledons. In the study, 4 bacterial OTUs and 15 fungal OTUs were found in germs, cotyledons, and sprouts simultaneously.

With the germination, the dominant bacterial genera *Halothiobacillus* and *Synechococcus* were still the most detected genera in spouts. Other bacterial genera *Erwinia*, *Hyphomonas*, and *Devosia* were detected in cotyledons and sprouts simultaneously. However, the bacterial genera except for *Hyphomonas* were not detected in peanut rhizosphere soils (Haldar et al. 2011). Some portions of endophytes might

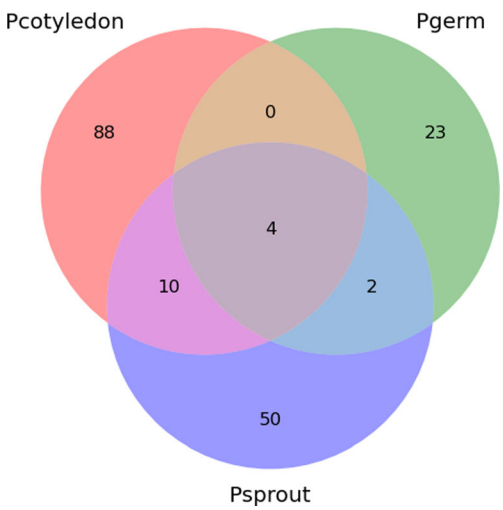

Fig. 1 Venn diagram illustration of the variation in bacterial OTUs of cotyledons (Pcotyledon), germs (Pgerm) of peanut seeds, and peanut sprouts (Psprout)

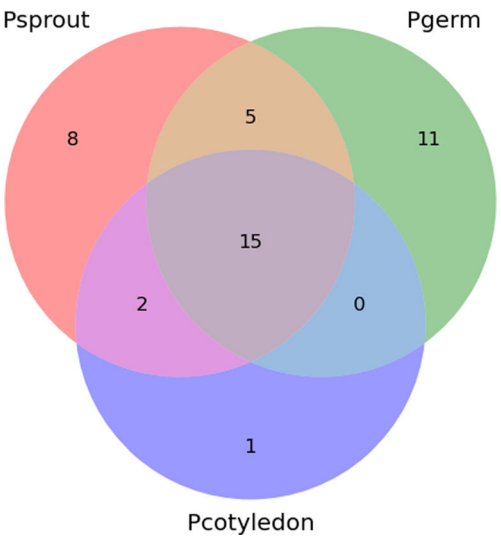

Fig. 2 Venn diagram illustration of the variation in fungal OTUs of cotyledons (Pcotyledon), germs (Pgerm) of peanut seeds, and peanut sprouts (Psprout)

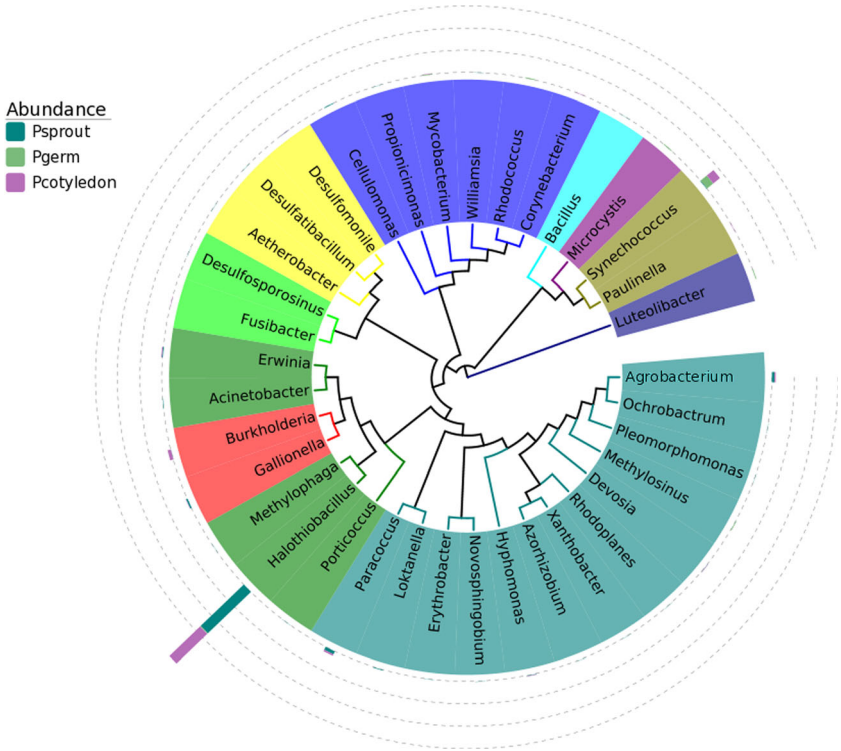

Fig. 3 Phylogenetic diagram of bacterial taxa OTUs of cotyledons (Pcotyledon), germs (Pgerm) of peanut seeds, and peanut sprouts (Psprout)

transmit from seeds, not from rhizosphere soils. The dominant fungal genera of germs, such as *Humicola*, *Emericella*, and *Penicillium*, were still detected in sprouts, and the *Emericella* was detected in sprouts, germs, and cotyledons, simultaneously. The *Humicola* and *Emericella* were still isolated from symptomless leaves of peanut (Suryanarayanan and Murali 2006), and the fungi might transmit from seeds because the leaves did have not contact with soils.

Co-inoculation of sulfur-oxidizing bacteria and *Rhizobium* could increase the dry weight, nodule number, plant biomass,

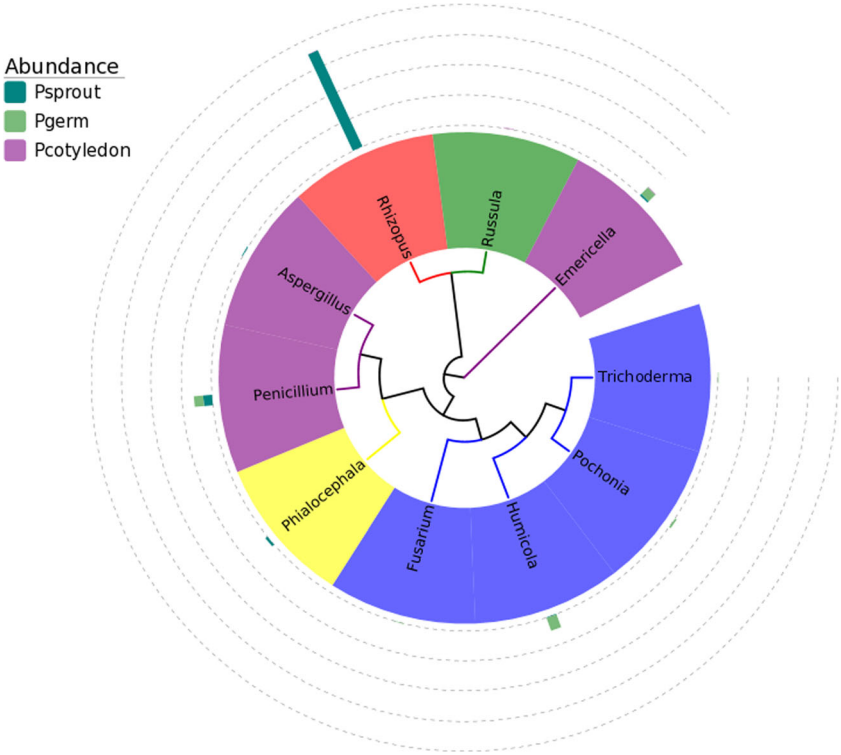

Fig. 4 Phylogenetic diagram of fungal taxa OTUs of cotyledons (Pcotyledon), germs (Pgerm) of peanut seeds, and peanut sprouts (Psprout)

Table 3 The growth promotion effects of *Halothiobacillus* SOB4 on peanut seedlings inoculated

	Seedlings without inoculation (controls)	Seedlings inoculated with SOB4*
Shoot length (cm)	8.9 ± 0.5a	12. 0 ± 0.6b
Shoot fresh weight (g)	5.4 ± 0.5a	9.9 ± 0.3b
Root fresh weight (g)	1.1 ± 0.3a	1.9 ± 0.1b

*Different letters (a and b) indicate the difference between seedlings inoculated with SOB4 and controls was significant ($P<0.05$)

and pod yield of peanut (Anandham et al. 2007). The fungal genera *Humicola* and *Emericella* in roots could solubilize soil phosphate and promote plant growth under salt stress or control plant disease (Sibounnavong et al. 2010). The *Halothiobacillus* could oxidize thiosulfate and solubilize soil phosphate, and are effective early plant growth-promoting rhizobacteria (Anandham et al. 2014). The *Halothiobacillus* as dominant bacterial genera was detected in germs, cotyledons, and sprouts, so the peanut plants contain core *Halothiobacillus.* In the study, the pot experiments showed that the isolated *Halothiobacillus* stain could promote the growth of peanut seedlings.

The previous studies have reported seed endophytes for many plants. However, still little is known on the persistence or existence of seed-borne endophytes across germination (Ferreira et al. 2008). It appeared that peanut has core mycobiome and bacteriome that is conserved across the germination from cotyledons and germ to sprouts and can be important sources of endophytes that colonize the mature plant. Based on the endophytic bacterial and fungal community in peanut cotyledons, germs, and sprouts, *Halothiobacillus* strain with growth promotion was isolated. Some novel species should be isolated by different methods. The procedure for beneficial endophytic strains is more feasible than traditional isolation and selection in greenhouse (Huang et al. 2016). The Illumina-based sequencing is suitable for rational isolation of beneficial endophytic strains to promote plant growth.

Acknowledgements This study was supported by Chinese National Natural Science Foundation (Grant No.: 31400111), Foundation for Distinguished Young Talents in Higher Education of Guangdong (Grant No.: 2013LYM-0011), Natural Science Foundation of Guangdong Province (Grant No.: 2015A030313355), and Youth Elite Project of Guangzhou University of Chinese Medicine (Grant No.: QNYC20170103).

References

Anandham R, Janahiraman V, Gandhi PI, Kwon SW, Chung KY, Han GH, Choi JH, Sa T (2014) Early plant growth promotion of maize by various sulfur oxidizing bacteria that uses different thiosulfate oxidation pathway. Afr J Microbiol Res 48:439–447

Anandham R, Sridar R, Nalayini P, Poonguzhali S, Madhaiyan M, Sa T (2007) Potential for plant growth promotion in groundnut (*Arachis hypogaea* L.) cv. ALR-2 by co-inoculation of sulfur-oxidizing bacteria and *Rhizobium*. Microbiol Res 162:139–153

Angelini J, Ibanez F, Taurian T, Tonelli ML, Valetti L, Fabra A (2011) A study on the prevalence of bacteria that occupy nodules within single peanut plants. Curr Microbiol 62:1752–1759

Fabra A, Castro S, Taurian T, Angelini J, Ibanez F, Dardanelli M, Tonelli M, Bianucci E, Valetti L (2010) Interaction among *Arachis hypogaea* L. (peanut) and beneficial soil microorganisms: how much is it known? Crit Rev Microbiol 36:179–194

Ferreira A, Quecine MC, Lacava PT, Oda S, Azevedo JL, Araújo WL (2008) Diversity of endophytic bacteria from species seeds and colonization of seedlings by *Pantoea agglomerans*. FEMS Microbiol Letters 287(1):8–14

Goldblatt LA (1971) Control and removal of aflatoxin. J Am Oil Chem Soc 48:605–610

Goncalez E, Nogueira JHC, Fonseca H, Felicio JD, Pino FA, Correa B (2008) Mycobiota and mycotoxins in Brazilian peanut kernels from sowing to harvest. Int J Food Microbiol 123: 184–190

Haldar S, Choudhury SR, Sengupta S (2011) Genetic and functional diversities of bacterial communities in the rhizosphere of *Arachis hypogaea*. Ant Leeuwenhoek 100:161–170

Huang YL, Kuang ZY, Wang WF, Cao LX (2016) Exploring potential bacterial and fungal biocontrol agents transmitted from seeds to sprouts of wheat. Biol Control 98:27–33

Ibañez F, Angelini J, Taurian T, Tonelli ML, Fabra A (2009) Endophytic occupation of peanut root nodules by opportunistic Gammaproteobacteria. Syst Appl Microbiol 32:49–55

Ibañez F, Arroyo ME, Angelini J, Tonelli ML, Muñoz V, Ludueña L, Valetti L, Fabra A (2014) Non-rhizobial peanut nodule bacteria promote maize (*Zea may* L.) and peanut (*Arachis hypogaea* L.) growth in simulated crop rotation system. Appl Soil Ecol 84:208–212

Johnston-Monje D, Raizada MN (2011) Conservation and diversity of seed associated endophytes in *Zea* across boundaries of evolution, ethnography and ecology. PLoS One 6:e20396. doi:10.1371/journal.pone.0020396

Kemp PF, Aller JY (2004) Bacterial diversity in aquatic and other environments: what 16S rDNA libraries can tell us. FEMS Microbiol Ecol 47:161–177

Kishore GK, Pande S, Podile AR (2005) Phylloplane bacteria increase seedling emergence, growth and yield of field-growth groundnut (*Arachis hypogaea* L.) Lett Appl Microbiol 40:260–268

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M et al. (2013) Towards a unified paradigm for sequence-based identification of fungi. Mol Ecol: 225271–5277

Links MG, Demeke T, Gräfenhan T, Hill JE, Hemmingsen SM, Dumonceaux TJ (2014) Simultaneous profiling of seed-associated bacteria and fungi reveals antagonistic interactions between microorganisms within a shared epiphytic microbiome on *Triticum* and *Brassica* seeds. New Phytol 202:542–553

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37:634–663

Nakai VK, Rocha LO, Goncalez E, Fonseca H, Ortega EMM, Correa B (2008) Distribution of fungi and aflatoxins in a stored peanut variety. Food Chem 106:285–290

Nicolaisen M, Justesen AF, Knorr K, Wang J, Pinnschmidt HO (2014) Fungal communities in wheat grain show significant co-existence patterns among species. Fungal Ecol 11:145–153

Ondov BD, Bergman NH, Phillippy AM (2011) Interactive metagenomic visualization in a Web browser. BMC Bioinform 12:385

Palencia ER, Hinton DM, Bacon CW (2010) The black *Aspergillus* species of maize and peanuts and their potential for mycotoxin production. Toxin 2:399–416

Park B, Shin WS, Chung JS (2008) Simultaneous biofiltration of H_2S, NH_3 and toluene using an inorganic/polymeric composite carrier. Environ Eng Res 13:19–27

Shi J, Lin H, Yuan X, Zhao Y (2011) Isolation and characterization of a novel sulfur-oxidizing chemolithoautotroph *Halothiobacillus* from Pb polluted paddy soil. Afr J Biotechnol 10:4121–4126

Sibounnavong P, Keoudone C, Soytong K, Divina CC, Kalaw SP (2010) A new mycofungicide from *Emericella nidulans* against tomato wilt caused by *Fusarium oxysporum* f. sp. *lycopersici* in vivo. J Agr Technol 6:19–30

Sobolev VS, Orner VA, Arias RS (2013) Distribution of bacterial endophytes in peanut seeds obtained from axenic and control plant material under field conditions. Plant Soil 371:367–376

Sorokin DY, Tourova TP, Lysenko AM, Muyzer G (2006) Diversity of culturable halophilic sulfur-oxidizing bacteria in hypersaline habitats. Microbiology 152:3013–3023

Suryanarayanan TS, Murali TS (2006) Incidence of *Leptosphaerulina crassiasca* in symptomless leaves of peanut in southern India. J Basic Microbiol 46:305–309

Taurian T, Anzuay MS, Angelini JG, Tonelli ML, Luduena L, Pena D, Ibanez F, Fabra A (2010) Phosphate-solubilizing peanut associated bacteria: screening for plant growth-promoting activities. Plant Soil 329:421–431

Truyens S, Weyens N, Cuypers A, Vangronsveld J (2015) Bacterial seed endophytes: genera, vertical transmission and interaction with plants. Environ Microbiol Rep 7:40–50

Wang K, Yan P, Ding Q, Wu Q, Wang Z, Peng J (2012) Diversity of culturable root-associated/endophytic bacteria and their chitinolytic and aflatoxin inhibition activity of peanut plant in China. World J Microbiol Biotechnol 29:1–10