Plant Soil (2015) 393:21–33
DOI 10.1007/s11104-015-2474-9

REGULAR ARTICLE

Soils naturally suppressive to banana *Fusarium* wilt disease harbor unique bacterial communities

Zongzhuan Shen · Yunze Ruan · Chao Xue · Shutang Zhong · Rong Li · Qirong Shen

Received: 14 October 2014 / Accepted: 8 April 2015 / Published online: 16 April 2015

Abstract
Aims Banana *Fusarium* wilt disease is caused by the *Fusarium oxysporum* f. sp. *cubense* race 4 fungus and is a vast problem for global banana production. Suppressive and conducive soils were analyzed to characterize important microbial populations and soil chemical properties that contribute to disease suppressiveness.
Methods Soil bacteria communities from the two banana orchards with excellent *Fusarium* disease suppression (suppressive soil) after long-term monoculture and two adjacent banana orchards with serious *Fusarium* wilt disease (conducive soils) were compared using deep 16S RNA barcode pyrosequencing.
Result Compared to the conducive soils within the same field site, higher ($P<0.05$) richness and diversity indices were observed in both suppressive soils. Moreover, more operational taxonomic units (OTUs) were observed in the two suppressive soils. Hierarchical cluster analyses showed that bacterial community membership and structure in disease-suppressive soils differed from disease-conducive soils. The *Acidobacteria* phylum was significantly ($P<0.05$) elevated, but *Bacteroidetes* was significantly ($P<0.05$) reduced in suppressive soils. The *Gp4*, *Gp5*, *Chthonomonas*, *Pseudomonas*, and *Tumebacillus* genera were significantly ($P<0.05$) enriched in suppressive soils, but *Gp2* was significantly ($P<0.05$) reduced in suppressive soils. Furthermore, the enrichment of *Gp5* and *Pseudomonas* as well as the soil physicochemical properties of available phosphorus were significantly ($P<0.05$) correlated with disease suppression.
Conclusions Naturally disease suppressive soils to banana *Fusarium* wilt disease harbor unique bacterial communities.

Keywords *Fusarium* wilt disease suppressive soil · Bacterial community · 16S rRNA pyrosequencing · Soil chemical properties · General suppression

Responsible Editor: Jeff R. Powell .

Zongzhuan Shen and Yunze Ruan contributed equally to this work.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-015-2474-9) contains supplementary material, which is available to authorized users.

Z. Shen · C. Xue · S. Zhong · R. Li (✉) · Q. Shen
Jiangsu Key Lab and Engineering Center for Solid Organic Waste Utilization, National Engineering Research Center for Organic-based Fertilizers, Key Laboratory of Plant Nutrition and Fertilization in Low-Middle Reaches of the Yangtze River, Ministry of Agriculture, Jiangsu Collaborative Innovation Center for Solid Organic Waste Resource Utilization, Nanjing Agricultural University, 210095 Nanjing, China
e-mail: lirong@njau.edu.cn

Y. Ruan
Hainan key Laboratory for Sustainable Utilization of Tropical Bio-resources, College of Agriculture, Hainan University, 570228 Haikou, China

Introduction

Microorganisms play a major role in the development and maintenance of soil health, an important

requirement for plant production in agricultural systems (Oros-Sichler et al. 2007). Furthermore, intrinsic microbial communities or specific sub-populations have the potential to suppress pathogen infectivity of host plants. This is a characteristic of disease-suppressive soils, where disease severity or incidence remains low, even in the presence of pathogens, susceptible host plants, and climatic conditions favorable for disease development (Alabouvette 1986; Baker and Cook 1974). Innate disease suppression in agricultural soils has been explored in multiple pathogen-plant systems, including *Streptomyces* spp. of potato (Meng et al. 2012), *Gaeumannomyces graminis* of wheat (Cook and Rovira 1976), and *Fusarium oxysporum* of melon (Peng et al. 1999). Few studies have focused on disease-suppressive soils to *Fusarium* wilt (Domínguez et al. 2003; Peng et al. 1999) with little data focusing on soil microbial community composition, especially at a finer resolution.

Banana is one of the most important cash crops in South China and *Cavendish* banana production comprises approximately 90 % of banana cultivars (Chen et al. 2013). Banana *Fusarium* wilt disease, caused by the *Fusarium oxysporum* f. sp. *cubense* race 4 fungal pathogen, has been reported to be the most limiting factor in *Cavendish* banana production worldwide since 1996 (Pegg et al. 1996). This disease is pervasive in China, resulting in vast economic losses (Butler 2013; Xu et al. 2011). Disease-suppressive banana orchards that maintain a low banana *Fusarium* wilt disease incidence (<15 %) over consecutive production years, paired with high disease incidence fields, have been identified on Hainan Island, China.

Bacteria, the most abundant and diverse group of soil organisms, influence the biological, chemical, and physical processes that drive terrestrial ecosystems. Thus, changes in microbial community composition or abundances of sub-populations can be indicators for disease suppression (Cook and Rovira 1976; Wu et al. 2008). Some indigenous bacteria in disease suppressive soils, such as *Pseudomonas*, *Bacillus*, and *Burkholderia*, have been shown to protect susceptible crops from soil-borne phytopathogens (de Boer et al. 2003; Kyselková et al. 2009; Larkin and Fravel 1998; Wang et al. 2013). Thus, characterization of the banana-associated soil microbial community in disease-suppressive soils using deep sequencing provides a foundation for soil community manipulation and eventual sustainable alternate pathogen control strategies (Rosenzweig et al. 2012).

However, while disease control may be largely attributed to the biological interactions between antagonistic microflora and pathogens through antibiotic production or enzymatic activities (Boudreau and Andrews 1987). There exist multiple indirect mechanisms related to general suppression that are induced by total microbial activity (Mazzola 2002). Lastly, although soil microbial composition is believed to be one of the primary drivers in soil-borne disease suppression, soil chemical properties may also be involved in plant diseases suppression (Garbeva et al. 2004).

In this study, we hypothesize that different types of disease-suppressive soils share a common bacterial community "core", which may be useful as indicator of disease-suppression. Therefore, the aims of this study are to: 1) compare the composition and structure of the bacterial community in disease suppressive and conducive soils; 2) identify key soil chemical properties in disease suppression and their correlations to bacterial community composition; and 3) explore the relationships between whole bacterial community composition or the presence of prevalent taxa with *Fusarium* wilt disease suppression.

Materials and methods

Field description

Two field sites differing in location, soil type, climate, and planting time were selected. The soils from the south field site, located in Jianfeng in southern Hainan Island, are dry red soils. Soils from the north field site located in Fushan, northern Hainan Island, are laterit soils. A continuously cropped banana orchard over the last 14 years in the south field site with sustained low *Fusarium* wilt disease incidence (14 % in 2012), was denoted as the disease-suppressive orchard with one treatment (SS). A co-located orchard with high *Fusarium* wilt disease incidence (62 % in 2012), also planted with banana for 14 years, was referred to as the "control" disease-conducive orchard (SC). A suppressive banana orchard in the north site with continuously low *Fusarium* wilt disease incidence (10 % in 2012) and a disease-conducive banana orchard with high *Fusarium* wilt disease incidence (68 % in 2012), both planted with banana for 12 years, were selected as treatment (NS) and control (NC), respectively. Management practices, including the banana cultivar

(*Musa acuminate* AAA *Cavendish* cv. Brazil), planting density (2550 tissue culture seedlings per ha), fertilization and irrigation, were all similar in the two paired orchards (Table 1).

Soil sampling and DNA extraction

Triplicate samples from each orchard soil were collected in August 2012 according to a modified method described by Shen et al. (2013). Briefly, 5 individual banana trees at least 5 m apart were selected for one sample collection, and the collected soil samples from each tree were mixed as a composite soil sample. For each tree, a composite soil sample from 4 sites under the trunk base was collected using a 25-mm soil auger to a depth of 20 cm. After sifting the samples through a 2 mm sieve and thoroughly homogenizing the samples, one portion of each sample was air-dried for chemical property analysis, and the other portion was stored at −70 °C for subsequent DNA extraction. Total soil genomic DNA was extracted using the PowerSoil DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, USA) following the manufacturer's instructions. The concentration and quality of the DNA were determined with a spectrophotometer (NanoDrop 2000, Wilmington, USA).

Bacterial 16S rRNA amplification and pyrosequencing

The DNA extracted from each soil sample served as a template for amplification of the V4-V5 hypervariable regions of the 16S rRNA gene using primers 515F and 907R (Xu et al. 2012) (Table S1). This yielded an approximate 400-bp region of the 16S rRNA gene, which is appropriate for the accurate phylogenetic reconstruction of bacteria (Biddle et al. 2008). All 16S rRNA amplifications for each sample were performed in a 50 μl mixture containing 45 μl of Platinum PCR SuperMix (Invitrogen Company, Shanghai, China), 200 nM final concentration of each primer, and 20 ng of template DNA. The PCR conditions included an initial denaturation step of 94 °C for 5 min followed by 28 cycles of denaturation at 94 °C for 45 s, annealing at 55 °C for 30 s, and extension at 72 °C for 45 s with a final extension at 72 °C for 5 min. The PCR products were purified using a 2.0 % agarose gel and quantified using Picogreen (Invitrogen Company, Shanghai, China). The amplicons from each sample were then pooled in an equimolar concentration into a single tube and an emulsion PCR was performed to generate the single strands on beads as required for 454 barcode pyrosequencing. Pyrosequencing was performed on the Roche 454 GS-FLX Titanium platform at Tongji-SCBIT Biotechnology Co., Ltd (Shanghai, China).

Pyrosequencing data processing

After pyrosequencing, raw data were processed by following the standard operating procedure described by Schloss et al. (2009) in Mothur. Briefly, sequences with a minimum flow length of 450 flows were denoised based on reimplementation of the PyroNoise algorithm with the default parameters (Quince et al. 2011). Sequences with more than 1 mismatch to the primer, any mismatch to the barcode, any ambiguous base call, homopolymers longer than 8 bases and reads shorter

Table 1 Detailed information of the four banana orchards

	NC	NS	SC	SS
Site	North	North	South	South
Latitude	19.831°N	19.833°N	18.651°N	18.645°N
Longitude	109.919°E	109.920°E	108.788°E	108.796°E
Temperature (°C)[a]	23	23	24	24
Precipitation (mm)[b]	2250	2250	1150	1150
Monocultured year	12	12	14	14
Disease incidence (%)[c]	68	10	62	14
Soil type	Laterit	Laterit	Dry red	Dry red

[a] The annual mean temperature of year 2011

[b] The annual mean precipitation of year 2011

[c] Disease incidence here represents the mean banana *Fusarium* wilt disease incidence of year 2012 for each treatment

than 250 bases were eliminated, and the filtered sequences were trimmed and assigned to soil samples based on barcodes. After removing the barcode and primer sequences, sequences were aligned against the Silva bacterial database (Pruesse et al. 2007). After screening, filtering, preclustering, and chimera removal, the retained sequences were used to build a distance matrix with a distance threshold of 0.2. Using the average neighbor algorithm with a cut-off of 97 % similarity, bacterial sequences were clustered to operational taxonomic units (OTUs), and the representative sequence for each OTU was selected and classified using a Ribosomal Database Project naive Bayesian rRNA classifier with a confidence threshold of 80 % (Wang et al. 2007).

A randomly selected subset of 5,409 sequences per sample was chosen for further bacterial community analysis in Mothur (Schloss et al. 2009). An OTU-based approach was performed to calculate the richness and diversity at an OTU distance of 0.03. Rarefaction was created to compare relative levels of bacterial OTU richness across all soil samples. Richness indices of the abundance based on coverage estimator (ACE) were calculated to estimate the number of OTUs present. Diversity within each individual sample was estimated using the nonparametric Shannon diversity index. To compare bacterial community membership and structures across all samples, a hierarchical cluster tree was constructed using the weighted and unweighted UniFrac metric matrices. To compare bacterial community composition between disease-suppressive and disease-conducive soil samples, a Venn diagram was generated based on the shared OTU table from the subsample after removing singletons (OTUs represented once with only one sequence in all samples).

Determination of soil chemical properties

Soil pH was measured using a glass electrode meter in a soil water suspension (1:2.5 w/v) after shaking for 30 min. Electrical conductivity (EC) was measured using a conductivity meter in a soil water suspension (1:5 w/v) after shaking for 30 min. The total organic carbon (TOC), total nitrogen (TON) and carbon to nitrogen ratio (C/N) were determined by a dry combustion method using an Element Analyzer (Vario EL, Germany). Available phosphorus (AP) in the soil was extracted with sodium bicarbonate and then determined using the molybdenum blue method. Available potassium (AK) in the soil was extracted with ammonium acetate and determined by flame photometry (Shen et al. 2013).

Statistical analysis

All data were tested for normality and homogeneity in IBM SPSS Statistics 20.0 and the data were transformed when necessary to meet the criteria for a normal distribution. Permutational multivariate analysis of variance (PERMANOVA) was performed to evaluate the significant differences of microbial community composition according to field sites, health status and the interaction of field sites with healthy status (Anderson 2001). All measured soil environmental variables were selected by forward selection in CANOCO 4.5 to determine the predictor variables (Etten 2005). Then, redundancy analysis (RDA) was performed using CANOCO 4.5 for Windows to examine the relationship among frequencies of abundant phyla, samples and selected soil variables. One-way analysis of variance (ANOVA) based on Duncan's multiple range test (DUNCAN) were performed for multiple comparisons and $P<0.05$ was considered to be statistically significant. Multiple linear regression was calculated using IBM SPSS Statistics 20.0 to determine the relationship of measured soil chemical properties with disease incidence and abundant phyla distribution.

Accession number

All raw sequences have been deposited at the DNA Data Bank of Japan (DDBJ) with accession number DRA002235.

Results

Sequencing results

After quality filtering, the pyrosequencing-based analysis of the V4 region of the 16S rRNA genes resulted in the recovery of 88,422 high quality sequences across all 12 samples. The number of high quality sequences within the bacterial domain per sample ranged from 5,409 to 14,790 with an average of 7,369 (Table S2). After re-sampling, there were 6,374 distinct OTUs observed at 3 % dissimilarity for 64,908 sequences among all soil subsamples (Table S3). In total, 50.4 % (3,213)

of all OTUs with 3,213 sequences were considered as singletons.

Bacterial community richness and diversity

Although the curves did not reach saturation, rarefaction curves of the mean pooled sequences for 3 replicates in each treatment at 3 % dissimilarity were compared and similar results were observed for disease-suppressive and disease-conducive soil samples from the same field site (Fig. 1). For both the south and north sites, higher OTU numbers were observed in soil samples collected from disease-suppressive orchards than from disease-conducive orchards.

Bacterial community richness and diversity were determined using the randomly re-sampled 5,409 sequences based on the ACE richness and the Shannon diversity (*H'*) index (Table 2). Significantly ($P<0.05$) higher bacterial richness and diversity were observed in SS soil samples than in SC soil samples in the south site, and though no difference was observed from the north site, richness and diversity values in the NS soil samples were both higher.

Bacterial community membership and structure

After removing singletons, 1,645 OTUs with 15,161 sequences and 1,553 OTUs with 15,501 sequences were observed in NS and NC soil samples while 1,718 OTUs with 15,347 sequences and 1,398 OTUs with 15,686 sequences were observed in SS and SC soil samples, respectively (Fig. 2 and Table S3). Soil samples collected from disease-suppressive banana orchards harbored a greater number of bacterial OTUs when compared to soil samples collected from disease-conducive banana orchards both in the same site and between different sites.

Hierarchical cluster analysis (Fig. 3), based on the weighted (Fig. 3a) and unweighted (Fig. 3b) UniFrac algorithm, revealed that bacterial community structure and membership collected from the same field sites were more similar when compared to different field sites. Hierarchical clusters from disease-suppressive soils were clearly separated from the disease-conducive soils, indicating contrasting bacterial community structures according to disease status.

Bacterial community composition

Fifteen bacterial phyla were identified in all samples with eight phyla, comprising 80 % of all sequences, were abundant (>1 %): *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, *Firmicutes*, *Nitrospirae*, *Planctomycetes*, and *Proteobacteria* (Fig. 4). Another seven phyla, including *Armatimonadetes*, *Chlamydiae*, *Cyanobacteria*, *Gemmatimonadetes*, *TM7*, *Verrucomicrobia*, and *WS3*, were in low abundance (<1 %). The highly affiliated phyla that did not appear in all soils were ascribed to "others" (Table S4). Overall, PERMANOVA revealed significant differences at the phylum composition according to field site ($F=191.07$, $P<0.05$) and health status ($F=13.21$, $P<0.05$), but no significantly to interaction term of the field with health status. Among the abundant phyla, a higher ($P<0.05$) abundance of *Acidobacteria* was in soil samples collected from disease-suppressive orchards compared to disease-conducive orchards within the same field site, while an opposite tendency was found for *Bacteroidetes*. However, the other abundant phyla did not show a consistent tendency in the south and north field sites.

The relative abundances of classified abundant genera (>1 %) for each soil sample that exhibited significant difference among banana orchards with different disease incidences were identified (Table 3). Among the most frequent, only 3 putative genera, namely *Gp1*, *Gp3*, and *Nitrospira*, were represented in all treatments. Only 9 and 8 of the most frequent putative genera were observed in the NC and SC soil samples, respectively, whereas 11 and 14 of the most frequent classified genera were observed in the NS and SS soil samples, respectively. Overall, PERMANOVA showed significant differences at the genus level composition according to field sites ($F=29.50$, $P<0.05$), health status ($F=5.59$, $P<0.05$) and the field with health status interaction term ($F=5.96$, $P<0.05$). The abundances of *Chthonomonas*, *Gp4*, *Gp5*, *Pseudomonas*, and *Tumebacillus* were higher ($P<0.05$) in the disease-suppressive soil samples than in disease-conducive soil samples within the same field site while the frequency of *Gp2* exhibited an opposite tend. Further multiple linear regression analyses revealed that the model, including *Gp5* and *Pseudomonas*, was a good predicator variable in disease incidence (Table S5).

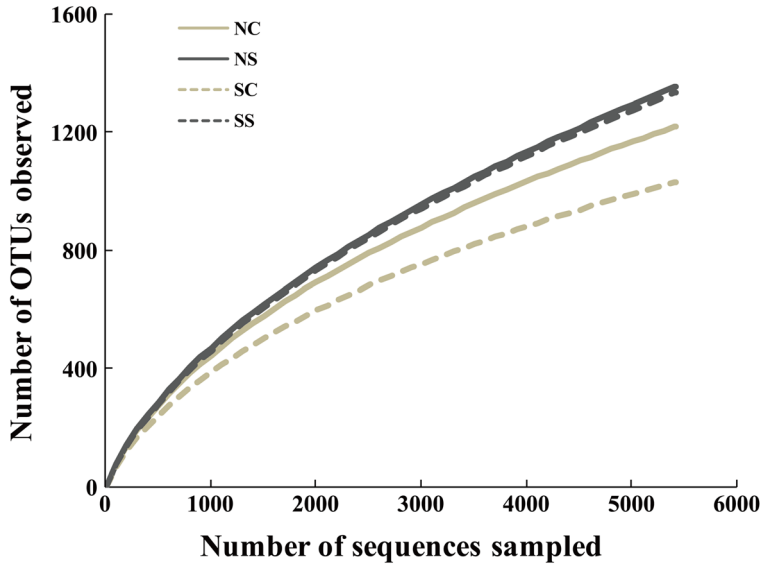

Fig. 1 Rarefaction analysis at 3 % dissimilarity levels for conducive soil samples collected from the north site (NC), suppressive soil samples collected from the north site (NS), conducive soil samples collected from the south site (SC) and suppressive soil samples collected from the south site (SS)

Effects of soil environmental variables on abundant phyla

The total soil carbon (TOC), total nitrogen (TON), C/N ratio (C/N), EC, pH, available phosphorus (AP), and available potassium (AK) for soil samples varied significantly in different banana orchards (Table 4). Values of TON, TOC, C/N and AK were higher ($P<0.05$) in soil samples collected from the north site (NS and NC) than from the south site (SS and SC), but pH, AP and EC did not show such tendency. Interestingly, both in the south and north sites, soil pH, AP and AK were higher ($P<0.05$) in disease-suppressive soil samples than in disease-conducive soil samples. Multiple linear regression analyses revealed that only AP was a significant predicator variable for disease incidence ($R=-0.392$, $P<0.05$).

Table 2 Richness (ACE) and diversity (Shannon) indices for the four banana orchards

Treatments	ACE	Shannon
NC	3213 (580)^{a}	6.06 (0.06)^{a}
NS	4151 (825)^{a}	6.19 (0.10)^{a}
SC	2390 (244)^{b}	5.48 (0.04)^{c}
SS	3717 (652)^{a}	6.02 (0.03)^{ab}

Values are means followed by one standard error of mean in parentheses. Different letters in each column indicates statistically significant differences at the 0.05 probability level according to the Duncan test

The environmental variables model, including field site, EC and available P, significantly explained the variation within the phyla data ($P=0.002$; Monte Carlo test) after stepwise selection. The RDA performed on selected soil environmental variables and abundant phyla data showed that the first and second RDA components explained 98.2 % of the total bacteria phyla variation (Fig. 5). The first component (RDA1) could separate soil treatments from different type soils, and the second component (RDA2) could separate disease-suppressive soil samples from disease-conducive soil samples within the same type soil.

Multiple linear regression was also used to evaluate relationships between abundant phyla and environmental variables (Table 5). Among the all measured environmental variables, TON and TOC was not correlated to any abundant phyla abundance. Among the predicator variables, field site was correlated to the relative abundances of *Acidobacteria*, *Chloroflexi*, *Nitrospirae*, *Planctomycetes* and *Proteobacteria* and soil EC was correlated to the relative abundances of *Acidobacteria* and *Nitrospirae*. Moreover, soil AP was correlated to the relative abundances of *Acidobacteria*, *Chloroflexi* and *Proteobacteria*.

Discussion

The existence of disease-suppressive soils has long been recognized, and attempts to elucidate the mechanisms

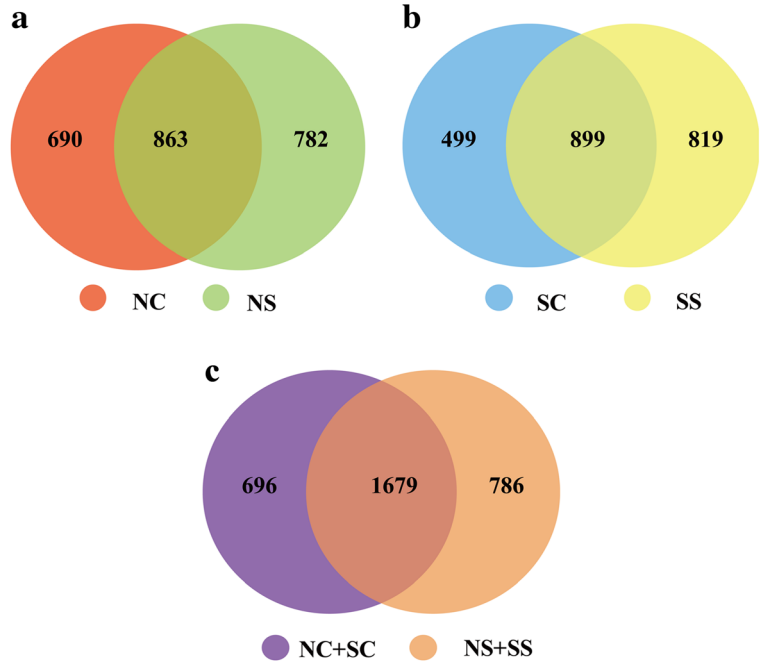

Fig. 2 Venn diagram for conducive soil samples (NC) and suppressive soil samples (NS) collected from the north site (**a**), for conducive soil samples (SC) and suppressive soil samples (SS) collected from the south site (**b**), and for conducive soil samples (NC+SC) and suppressive soil samples (NS+SS) collected different sites (**c**) showing shared and unique OTUs based on the OTU shared table at 0.03 dissimilarity distances after removing singletons

involved in soil-borne disease suppression have yielded information on numerous potential biological control agents (Alabouvette et al. 1996). In this study, microbial communities from banana *Fusarium* wilt disease-conducive and disease-suppressive soils were analyzed for the presence of signature organisms indicative of functional suppression. The observation of richer, more diverse bacterial communities in our disease-suppressive soils is supported by earlier findings that also revealed higher diversity in suppressive soils or those with the addition of bio-organic fertilizer (Qiu et al. 2012; Zhang et al. 2013; Zhao et al. 2011). Furthermore, though not significant, a large number of OTUs were recovered from the disease-suppressive soils, also in agreement with previous work reported by Rosenzweig et al. (2012), who found more OTUs in potato common scab-suppressive soils.

As revealed through hierarchical cluster analyses, field-scale spatial influences were pronounced with samples from the same field having more similar bacterial community structure, regardless of suppression status, similar to previous findings (Roesch et al. 2007; Lundberg et al. 2012). Within each field, suppression status resulted in significantly different bacterial

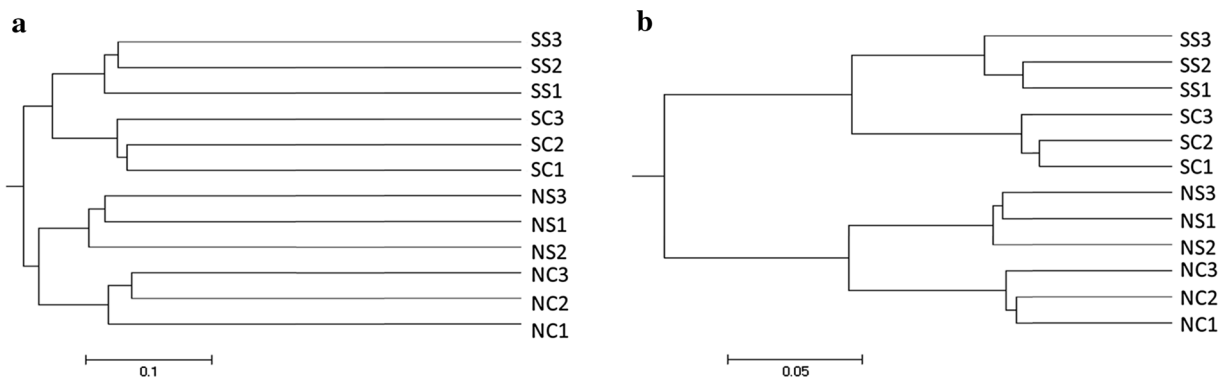

Fig. 3 Hierarchical cluster tree constructed based on the distance matrix that was calculated using the (a) weighted UniFrac algorithm and (b) unweighted UniFrac algorithm for conducive soil samples collected from the north site (NC), suppressive soil samples collected from the north site (NS), conducive soil samples collected from the south site (SC) and suppressive soil samples collected from the south site (SS)

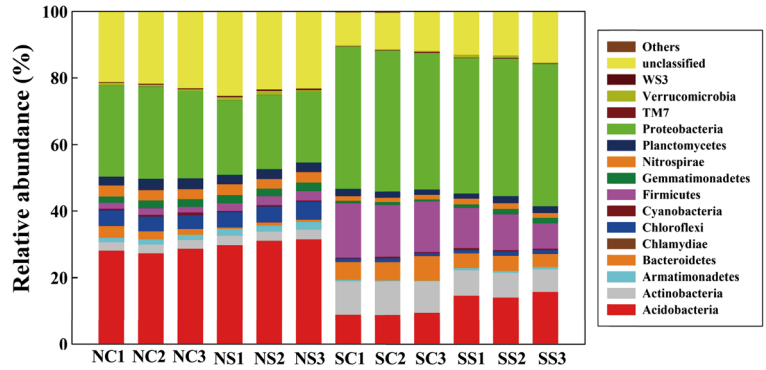

Fig. 4 The relative abundance of phyla for conducive soil samples collected from the north site (NC), suppressive soil samples collected from the north site (NS), conducive soil samples collected from the south site (SC) and suppressive soil samples collected from the south site (SS). "Others" indicates extremely low abundant phyla, including *Chlorobi*, *Elusimicrobia*, *Spirochaetes*, *Synergistetes*, *BRC1*, *OD1* and *OP11*

community composition, similar to previous studies that found suppressive soils for tobacco black root rot disease (Kyselková et al. 2009), *Rhizoctonia solani* AG8 bare patch disease (Penton et al. 2013), and cabbage clubroot disease (Hjort et al. 2007) harbored distinct communities.

Proteobacteria and *Acidobacteria* were the two most abundant phyla, followed by *Firmicutes*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, *Nitrospirae* and *Planctomycetes*, roughly corresponding to the bacterial community structure identified in agricultural or other soil types (Acosta-Martinez et al. 2008; Roesch et al. 2007). A

Table 3 Frequency of the most abundant classified bacterial genera (expressed as %) of all classified sequences within the four banana orchards

Genus	NC	NS	SC	SS
Pseudomonas	0.52 (0.07)^{c}	0.79 (0.14)^{b}	0.39 (0.07)^{d}	2.00 (0.31)^{a}
Gp5	0.20 (0.13)^{c}	1.17 (0.09)^{a}	0.14 (0.04)^{c}	0.40 (0.09)^{b}
Chthonomonas	0.88 (0.03)^{b}	1.62 (0.27)^{a}	0.16 (0.10)^{d}	0.36 (0.04)^{c}
Tumebacillus	0.03 (0.03)^{d}	0.12 (0.02)^{c}	0.85 (0.33)^{b}	1.48 (0.15)^{a}
Gp4	2.07 (0.27)^{b}	3.61 (0.39)^{a}	0.25 (0.06)^{c}	2.15 (0.13)^{b}
Gp2	2.59 (0.26)^{a}	2.14 (0.13)^{b}	0.40 (0.08)^{c}	0.18 (0.04)^{d}
Gp3	**2.12 (0.49)**^{b}	**3.82 (0.42)**^{a}	**1.46 (0.28)**^{c}	**1.46 (0.27)**^{c}
Gemmatimonas	2.23 (0.24)^{a}	2.42 (0.15)^{a}	0.73 (0.12)^{c}	1.42 (0.34)^{b}
Gp6	8.22 (0.40)^{a}	5.95 (0.11)^{b}	0.89 (0.21)^{c}	6.32 (0.89)^{b}
Steroidobacter	1.29 (0.17)^{a}	0.50 (0.20)^{b}	0.08 (0.02)^{c}	0.41 (0.08)^{b}
Nitrospira	**3.14 (0.16)**^{a}	**3.10 (0.19)**^{a}	**1.36 (0.02)**^{c}	**1.66 (0.20)**^{b}
Gp7	1.53 (0.20)^{a}	1.24 (0.12)^{b}	0.09 (0.05)^{d}	0.26 (0.05)^{c}
Rhizobium	0.08 (0.03)^{c}	0.05 (0.03)^{c}	0.88 (0.15)^{b}	1.34 (0.08)^{a}
Sphingobium	0.05 (0.04)^{c}	0.02 (0.00)^{c}	0.30 (0.10)^{b}	1.08 (0.12)^{a}
Planctomyces	0.95 (0.25)^{b}	1.19 (0.12)^{a}	0.25 (0.06)^{c}	0.31 (0.07)^{c}
Dokdonella	0.11 (0.02)^{c}	0.15 (0.05)^{c}	11.69 (0.66)^{a}	5.58 (0.15)^{b}
Bacillus	0.13 (0.01)^{c}	0.42 (0.11)^{b}	3.73 (0.59)^{a}	2.72 (0.99)^{a}
Flavobacterium	0.22 (0.02)^{b}	0.04 (0.04)^{c}	1.49 (0.20)^{a}	1.41 (0.23)^{a}
Rhodanobacter	0.02 (0.03)^{b}	0.00 (0.00)^{b}	1.80 (0.73)^{a}	1.34 (0.69)^{a}
Microbacterium	0.01 (0.01)^{c}	0.00 (0.00)^{c}	1.09 (0.25)^{a}	0.26 (0.11)^{b}
Gp1	**9.38 (0.81)**^{a}	**9.73 (1.05)**^{a}	**4.80 (0.29)**^{b}	**2.39 (0.10)**^{c}

Values are means followed by one standard error of mean in parentheses. Different letters in each row indicates statistically significant differences at the 0.05 probability level according to the Duncan test. Three abundant genera as showing in bold are indentified in all soil samples

Table 4 Measured chemical properties of the soil samples from the four banana orchards

Treatment	pH	TON (g/kg)*	TOC (g/kg)*	C/N*	AP (mg/kg)	AK (mg/kg)*	EC (us/cm)*
NC	5.14 (0.08)^{d}	1.80 (0.02)^{a}	19.19 (0.08)^{a}	10.64 (0.13)^{a}	73.2 (0.19)^{d}	351 (12)^{b}	104 (6)^{c}
NS	6.68 (0.11)^{a}	1.52 (0.02)^{b}	14.98 (0.12)^{b}	9.83 (0.08)^{b}	231.38 (2.32)^{a}	553 (16)^{a}	48 (6)^{d}
SC	5.29 (0.05)^{c}	0.82 (0.01)^{d}	5.36 (0.22)^{d}	6.50 (0.16)^{d}	147.15 (3.75)^{c}	130 (2)^{d}	219 (6)^{b}
SS	5.58 (0.04)^{b}	0.94 (0.05)^{c}	7.45 (0.33)^{c}	7.92 (0.11)^{c}	164.19 (4.60)^{b}	172 (10)^{c}	355 (6)^{a}

Values are means followed by one standard error of mean in parentheses. Different letters in each column indicates statistically significant differences at the 0.05 probability level according to the Duncan test. * represents a statistically significant differences ($P<0.05$) between north (NC+NS) and south (SC+SS) soil samples according to two samples t-test

lower abundance of *Bacteroidetes* was observed in both disease-suppressive soils collected from the south and north field within the same site and agrees with lower abundances identified in other suppressive soils (Sanguin et al. 2009). In addition, the identification of higher abundances of *Acidobacteria* in our suppressive soils has also been observed in potato common scab suppressive soils (Rosenzweig et al. 2012). At a coarse taxonomic scale, these changes in *Acidobacteria* and *Bacteroidetes* abundances suggest a linkage to disease suppression. However, we found no significant correlation between phyla level bins and disease suppression, indicating that deeper taxonomic analyses are required.

Thus, the most abundant genera in each soil sample were investigated in detail, and significantly higher abundances of *Chthonomonas*, *Gp4*, *Gp5*, *Pseudomonas*, and *Tumebacillus* in both disease-suppressive soil samples were found, compared to the co-located conducive soil samples. *Pseudomonas* has been identified as a broad indicator of suppression of a variety of pathogens such as *Thielaviopsis basicola* (Kyselková et al. 2009), *Gaeumannomyces graminis*

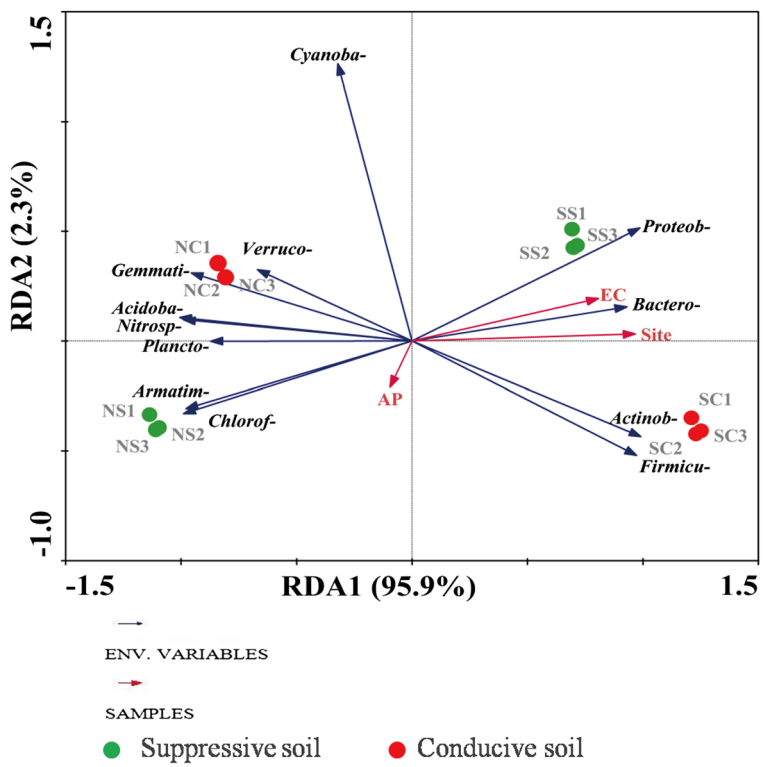

Fig. 5 Redundancy analysis (RDA) based on the relative abundance of bacterial phyla and selected environmental variables for conducive soil samples collected from the north site (NC), suppressive soil samples collected from the north site (NS), conducive soil samples collected from the south site (SC) and suppressive soil samples collected from the south site (SS). The following abbreviations are used: *Protrob-*, *Proteobacteria*; *Bactero-*, *Bacteroidetes*; *Actinob-*, *Actinobacteria*; *Firmicu-*, *Firmicutes*; *Cyanoba-*, *Cyanobacteria*; *Gemmati-*, *Gemmatimonadetes*; *Acidoba-*, *Acidobacteria*; *Plancto-*, *Planctomycetes*; *Nitrosp-*, *Nitrospira*; *Armatim-*, *Armatimonadetes*; *Verruco-*, *Verrucomicrobia*; *Chlorof-*, *Chloroflexi*; AP, soil available phosphorus; EC, electricity conductivity; Site, field site

Table 5 Multiple regression coefficient (r) between abundant phyla and environmental variables for all soil samples collected from the four different banana orchards

Phylum	pH	TON	TOC	CN	AP	AK	EC	Site
Acidobacteria	NS	NS	NS	NS	0.19	NS	0.49	−1.41
Actinobacteria	−0.16	NS	NS	−0.94	NS	NS	NS	NS
Bacteroidetes	NS	NS	NS	NS	NS	−0.93	NS	NS
Chloroflexi	−0.61	NS	NS	0.33	1.22	−1.18	NS	−2.02
Firmicutes	NS	NS	NS	NS	NS	NS	NS	NS
Nitrospira	NS	NS	NS	NS	NS	NS	0.31	−0.15
Planctomycetes	NS	NS	NS	NS	NS	NS	NS	−0.90
Proteobacteria	NS	NS	NS	NS	−0.20	NS	NS	0.98

NS means the environmental variable is not included in the model and removed by the stepwise analyses

(Bull et al. 1991), *Pythium splendens* (Buysens et al. 1996), *Phytophthora infestans* (Tran et al. 2007), *Agrobacterium tumefaciens* (Dandurishvili et al. 2011), and *Rhizoctonia solani* (Berta et al. 2005). Among others, *Gp4* and *Gp5* have also been found in higher abundances in potato common scab-suppressive soil caused by *Streptomyces* spp. (Rosenzweig et al. 2012). Little physiological data exists for the two relatively new genera *Tumebacillus* (*Firmicutes*) and *Chthonomonas* (*Armatimonadetes*) (Steven et al. 2008; Lee et al. 2011). As such, their ecological role in the soil is still unclear.

After regression analyses, *Gp5* and *Pseudomonas* were found to be most associated with disease suppression of banana *Fusarium* wilt. Specifically, *Pseudomonas* has frequently been reported to be responsible for the natural suppression of *Fusarium* wilt disease and it has been utilized for banana *Fusarium* wilt disease biocontrol (Kavino et al. 2010; Saravanan et al. 2004; Sivamani and Gnanamanickam 1988) likely by their: 1) production of a wide spectrum of bioactive metabolites, 2) rapid utilization of root exudates, 3) colonization and multiplication in the environment, and 4) aggressive competition with other microorganisms (Kloepper et al. 1980; Lemanceau and Alabouvette 1993; Weller 1988). Although no direct antagonistic activities have been reported, *Acidobacteria* subgroup *Gp5* is a promising candidate subdivision for disease suppression. The subgroup has been detected at higher abundances in many disease-suppressives compared to disease-conducive soils (Hunter et al. 2006; Sanguin et al. 2009). Therefore, our results compounded with earlier studies suggest that *Pseudomonas* and the *Acidobacteria* subgroups may be important in the natural disease suppression of banana *Fusarium* wilt disease. However, whether this mechanism is through direct antagonism or resource competition, especially in the case of *Gp5*, is currently unknown and a subject for future research.

Results from Monte-Carlo tests revealed that soil environmental variables shaped the phylum-level bacterial community composition, in accordance with earlier studies that demonstrated strong influences of soil environmental variables (Acosta-Martinez et al. 2008; Peng et al. 1999; Domínguez et al. 2001). Overall, the field site location was the largest effect in determining bacterial composition in the current study, similar to previous works that illustrated the importance of spatial influences (Bossio et al. 1998; Girvan et al. 2003; Zhao et al. 2014). However, within the same field and across treatments, disease status overcame field site as a principle driver, emphasizing the importance of spatial scale in determining soil environmental variables on bacterial community structure. Higher soil AP was found in the two disease-suppressive compared to the disease-conducive soils within the same field site and a significant ($P<0.05$) negative correlation to disease incidence was also observed. This is similar to previous findings indicating that higher soil AP associated with lower wheat *Rhizoctonia* root rot disease incidence (Davey et al. 2012) and lower stem rot disease incidence caused by *Rhizoctonia solani* (Chauhan et al. 2000). The disease suppression may be due to that higher AP could stimulate plant growth then enhance host disease resistance to soil pathogens (Davey et al. 2012). Higher AK and pH in disease-suppressive versus in disease-

conducive soils within the same field site was observed, though no significant correlation to disease incidence was observed. This finding agrees with a previous report suggesting that soil AK is higher in banana *Fusarium* wilt disease-suppressive soils (Peng et al. 1999) and higher pH enhanced the *Fusarium* wilt disease suppression (Senechkin et al. 2014). Potassium impacts numerous physiological and biochemical processes that have relevance for plant susceptibility to pathogens, such as manipulation of specific metabolic enzymes and hormonal pathways to help the host against pathogen infection (Amtmann et al. 2008). Soil pH can influence plant disease suppression directly by effects on the soilborne pathogen and microorganisms and indirectly through soil nutrients availability to the plant host (Ghorbani et al. 2008).

However, very complex interactions between soil properties and abundant phyla were exhibited in our current study, confirming that it is generally difficult to demonstrate the exact mechanisms of abiotic factors involved in disease suppression (Höper and Alabouvette 1996; Alabouvette 1999). In addition, microbiological and enzymatic parameters are more indicative of disease suppression than chemical parameters in general (Bonanomi et al. 2010). Taking together, these findings suggest that higher pH, AP and AK may enhance the suppression ability to banana *Fusarium* wilt disease probably by impacting the composition and activity of the soil microbial communities and/or induce the resistance of banana itself (Mazzola 2002).

In conclusion, comparisons of soil bacterial communities from two natural banana *Fusarium* wilt-suppressive orchards showed that these disease-suppressive soils harbored distinctive bacterial communities, compared to their disease-conducive counterparts. Specifically, higher abundances of members within the *Acidobacteria* phylum, specifically *Gp4* and *Gp5*, and of the genera *Chthonomonas*, *Pseudomonas*, and *Tumebacillus* were identified while the *Bacteroidetes* were in decreased abundance in the disease-suppressive soils. Moreover, the enrichment of *Gp5* and *Pseudomonas* in addition to the soil physicochemical property AP were positively correlated with disease suppression. Although understanding the exact mechanisms for enhanced disease suppression driven by the composition of the microbial community or by specific populations is complex, this study reveals that banana *Fusarium* wilt suppressive soils harbor unique communities with higher richness and diversity and identified specific populations that may be considered as indicators of the ability of a soil to suppress disease.

Acknowledgments This research was supported by the National Key Basic Research Program of China (2015CB150506), the National Natural Science Foundation of China (31372142 and 41101231), the Department of Science and Technology of Hainan Province (ZDZX2013023), the Chinese Ministry of Science and Technology (2013AA102802), the Priority Academic Program Development of the Jiangsu Higher Education Institutions (PAPD), the 111 project (B12009), the Agricultural Ministry of China (201103004), National Key Technology R&D Program of the Ministry of Science and Technology (2011BAD11B03) and the Innovative Research Team Development Plan of the Ministry of Education of China (IRT1256).

References

Acosta-Martinez V, Dowd S, Sun Y, Allen V (2008) Tag-encoded pyrosequencing analysis of bacterial diversity in a single soil type as affected by management and land use. Soil Biol Biochem 40:2762–2770

Alabouvette C (1986) Fusarium-wilt suppressive soils from the Châteaurenard region: review of a 10-year study. Agronomie 6:273–284

Alabouvette C (1999) Fusarium wilt suppressive soils: an example of disease-suppressive soils. Australas Plant Pathol 28:57–64

Alabouvette C, Lemanceau P, Steinberg C (1996) Biological control of Fusarium wilts: opportunities for developing a commercial product. In: Hall R (ed) Principles and practice of managing soilborne plant pathogens. APS Press, St Paul, pp 192–212

Amtmann A, Troufflard S, Armengaud P (2008) The effect of potassium nutrition on pest and disease resistance in plants. Physiol Plant 133:682–691

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Baker KF, Cook RJ (1974) Biological control of plant pathogens. WH Freeman, San Francisco, p 433

Berta G, Sampo S, Gamalero E, Massa N, Lemanceau P (2005) Suppression of *Rhizoctonia* root-rot of tomato by *Glomus mossae* BEG12 and *Pseudomonas fluorescens* A6RI is associated with their effect on the pathogen growth and on the root morphogenesis. Eur J Plant Pathol 111:279–288

Biddle JF, Fitz-Gibbon S, Schuster SC, Brenchley JE, House CH (2008) Metagenomic signatures of the Peru Margin subseafloor biosphere show a genetically distinct environment. Proc Natl Acad Sci U S A 105:10583–10588

Bonanomi G, Antignani V, Capodilupo M, Scala F (2010) Identifying the characteristics of organic soil amendments that suppress soilborne plant diseases. Soil Biol Biochem 42:136–144

Bossio DA, Scow KM, Gunapala N, Graham KJ (1998) Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microb Ecol 36:1–12

Boudreau MA, Andrews JH (1987) Factors influencing antagonism of *Chaetomium globosum* to *Venturia inaequalis*: a case study in failed biocontrol. Phytopathology 77:1470–1475

Bull CT, Weller DM, Thomashow LS (1991) Relationship between root colonization and suppression of *Gaeumannomyces* graminis var. tritici by *Pseudomonas fluorescens* strain 2–79. Phytopathology 81:954–959

Butler D (2013) Fungus threatens top banana. Nature 504:195–196

Buysens S, Heungens K, Poppe J, Hofte M (1996) Involvement of pyochelin and pyoverdin in suppression of *Pythium*-induced damping-off of tomato by *Pseudomonas aeruginosa* 7NSK2. Appl Environ Microb 62:865–871

Chauhan R, Maheshwari S, Gandhi S (2000) Effect of nitrogen, phosphorus and farm yard manure levels on stem rot of cauliflower caused by *Rhizoctonia solani* Kuhn. Agric Sci Dig 20:36–38

Chen YF, Chen W, Huang X, Hu X, Zhao JT, Gong Q, Li XJ, Huang XL (2013) Fusarium wilt-resistant lines of Brazil banana (*Musa* spp., AAA) obtained by EMS-induced mutation in a micro-cross-section cultural system. Plant Pathol 62: 112–119

Cook RJ, Rovira A (1976) The role of bacteria in the biological control of *Gaeumannomyces graminis* by suppressive soils. Soil Biol Biochem 8:269–273

Dandurishvili N, Toklikishvili N, Ovadis M, Eliashvili P, Giorgobiani N, Keshelava R, Tediashvili M, Vainstein A, Khmel I, Szegedi E, Chernin L (2011) Broad-range antagonistic rhizobacteria *Pseudomonas fluorescens* and *Serratia plymuthica* suppress *Agrobacterium* crown gall tumours on tomato plants. J Appl Microbiol 110:341–352

Davey R, McNeill A, Gupta V, Barnett S (2012) Rhizoctonia root rot suppression in an alkaline calcareous soil from a low rainfall farming system. In: Yunusa I (ed) "Capturing opportunities and overcoming obstacles in Australian agronomy". Proceedings of 16th Australian Agronomy Conference, 14–18 October 2012, Armidale, NSW

de Boer M, Bom P, Kindt F, Keurentjes JJ, van der Sluis I, Van Loon L, Bakker PA (2003) Control of Fusarium wilt of radish by combining *Pseudomonas putida* strains that have different disease-suppressive mechanisms. Phytopathology 93:626–632

Domínguez J, Negrín M, Rodríguez C (2001) Aggregate water-stability, particle-size and soil solution properties in conducive and suppressive soils to Fusarium wilt of banana from Canary Islands (Spain). Soil Biol Biochem 33:449–455

Domínguez J, Negrín M, Rodríguez C (2003) Evaluating soil sodium indices in soils of volcanic nature conducive or suppressive to *Fusarium* wilt of banana. Soil Biol Biochem 35:565–575

Etten EV (2005) Multivariate analysis of ecological data using CANOCO. Austral Ecol 30:486–487

Garbeva P, Veen JA, Elsas JD (2004) Assessment of the diversity, and antagonism towards *Rhizoctonia solani* AG3, of *Pseudomonas* species in soil from different agricultural regimes. FEMS Microbiol Ecol 47:51–64

Ghorbani R, Wilcockson S, Koocheki A, Leifert C (2008) Soil management for sustainable crop disease control: a review. Environ Chem Lett 6:149–162

Girvan MS, Bullimore J, Pretty JN, Osborn AM, Ball AS (2003) Soil type is the primary determinant of the composition of the total and active bacterial communities in arable soils. Appl Environ Microb 69:1800–1809

Hjort K, Lembke A, Speksnijder A, Smalla K, Jansson JK (2007) Community structure of actively growing bacterial populations in plant pathogen suppressives soil. Microb Ecol 53: 399–413

Höper H, Alabouvette C (1996) Importance of physical and chemical soil properties in the suppressiveness of soils to plant diseases. Eur J Soil Biol 32:41–58

Hunter PJ, Petch GM, Calvo-Bado LA, Pettitt TR, Parsons NR, Morgan JAW, Whipps JM (2006) Differences in microbial activity and microbial populations of peat associated with suppression of damping-off disease caused by *Pythium sylvaticum*. Appl Environ Microb 72:6452–6460

Kavino M, Harish S, Kumar N, Saravanakumar D, Samiyappan R (2010) Effect of chitinolytic PGPR on growth, yield and physiological attributes of banana (*Musa* spp.) under field conditions. Appl Soil Ecol 45:71–77

Kloepper JW, Leong J, Teintze M, Schroth MN (1980) Pseudomonas siderophores: a mechanism explaining disease-suppressive soils. Curr Microbiol 4:317–320

Kyselková M, Kopecký J, Frapolli M, Défago G, Ságová-Marečková M, Grundmann GL, Moënne-Loccoz Y (2009) Comparison of rhizobacterial community composition in soil suppressive or conducive to tobacco black root rot disease. ISME J 3:1127–1138

Larkin RP, Fravel DR (1998) Efficacy of various fungal and bacterial biocontrol organisms for control of Fusarium wilt of tomato. Plant Dis 82:1022–1028

Lee KCY, Dunfield PF, Morgan XC, Crowe MA, Houghton KM, Vyssotski M, Ryan JL, Lagutin K, McDonald IR, Stott MB (2011) *Chthonomonas calidirosea* gen. nov., sp. nov., an aerobic, pigmented, thermophilic micro-organism of a novel bacterial class, *Chthonomonadetes* classis nov., of the newly described phylum *Armatimonadetes* originally designated candidate division OP10. Int J Syst Evol Microbiol 61: 2482–2490

Lemanceau P, Alabouvette C (1993) Suppression of fusarium wilts by fluorescent pseudomonads: mechanisms and applications. Biocontrol Sci Tech 3:219–234

Lundberg DS, Lebeis SL, Paredes SH, Yourstone S, Gehring J, Malfatti S, Tremblay J, Engelbrektson A, Kunin V, del Rio TG (2012) Defining the core *Arabidopsis thaliana* root microbiome. Nature 488:86–90

Mazzola M (2002) Mechanisms of natural soil suppressiveness to soilborne diseases. Anton Leeuw Int J G 81:557–564

Meng Q, Yin J, Rosenzweig N, Douches D, Hao JJ (2012) Culture-based assessment of microbial communities in soil suppressive to potato common scab. Plant Dis 96:712–717

Oros-Sichler M, Costa R, Heuer H, Small K (2007) Molecular fingerprinting techniques to analyze soil microbial communities. In: Elsas JV, Jansson J, Trevors J (eds) Modern soil microbiology, 2nd edn. CRC Press, Boca Raton, pp 355–386

Pegg K, Moore N, Bentley S (1996) Fusarium wilt of banana in Australia: a review. Aust J Agr Res 47:637–650

Peng HX, Sivasithamparam K, Turner DW (1999) Chlamydospore germination and Fusarium wilt of banana plantlets in suppressive and conducive soils are affected by physical and chemical factors. Soil Biol Biochem 31:1363–1374

Penton CR, Vadakattu VVSR, Tiedje JM, Ophel-Keller K, Neate SM, Gillings M, Harvey P, Roget DK (2013) Fungal

community structure in disease suppressive soils assessed by 28S LSU gene sequencing. PLoS One 9(4), e93893

Pruesse E, Quast C, Knittel K, Fuchs BM, Ludwig W, Peplies J, Glöckner FO (2007) SILVA: a comprehensive online resource for quality checked and aligned ribosomal RNA sequence data compatible with ARB. Nucleic Acids Res 35:7188–7196

Qiu MH, Zhang RF, Xue C, Zhang SS, Li SQ, Zhang N, Shen QR (2012) Application of bio-organic fertilizer can control *Fusarium* wilt of cucumber plants by regulating microbial community of rhizosphere soil. Biol Fertil Soils 48:807–816

Quince C, Lanzen A, Davenport RJ, Turnbaugh PJ (2011) Removing noise from pyrosequenced amplicons. BMC Bioinformatics 12:38

Roesch LF, Fulthorpe RR, Riva A, Casella G, Hadwin AK, Kent AD, Daroub SH, Camargo FA, Farmerie WG, Triplett EW (2007) Pyrosequencing enumerates and contrasts soil microbial diversity. ISME J 1:283–290

Rosenzweig N, Tiedje JM, Quensen JF III, Meng Q, Hao JJ (2012) Microbial communities associated with potato common scab-suppressive soil determined by pyrosequencing analyses. Plant Dis 96:718–725

Sanguin H, Sarniguet A, Gazengel K, Moënne-Loccoz Y, Grundmann G (2009) Rhizosphere bacterial communities associated with disease suppressiveness stages of take-all decline in wheat monoculture. New Phytol 184:694–707

Saravanan T, Muthusamy M, Marimuthu T (2004) Effect of *Pseudomonas fluorescens* on Fusarium wilt pathogen in banana rhizosphere. J Biol Sci 4:192–198

Schloss PD, Westcott SL, Ryabin T, Hall JR, Hartmann M, Hollister EB, Lesniewski RA, Oakley BB, Parks DH, Robinson CJ (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Appl Environ Microb 75:7537–7541

Senechkin IV, van Overbeek LS, van Bruggen AH (2014) Greater Fusarium wilt suppression after complex than after simple organic amendments as affected by soil pH, total carbon and ammonia-oxidizing bacteria. Appl Soil Ecol 73:148–155

Shen Z, Zhong S, Wang Y, Wang B, Mei X, Li R, Ruan Y, Shen Q (2013) Induced soil microbial suppression of banana fusarium wilt disease using compost and biofertilizers to improve yield and quality. Eur J Soil Biol 57:1–8

Sivamani E, Gnanamanickam S (1988) Biological control of *Fusarium oxysporum* f. sp. *cubense* in banana by inoculation with *Pseudomonas fluorescens*. Plant Soil 107:3–9

Steven B, Chen MQ, Greer CW, Whyte LG, Niederberger TD (2008) *Tumebacillus permanentifrigoris* gen. nov., sp. nov., an aerobic, spore-forming bacterium isolated from Canadian high Arctic permafrost. Int J Syst Evol Microbiol 58:1497–1501

Tran H, Ficke A, Asiimwe T, Höfte M, Raaijmakers JM (2007) Role of the cyclic lipopeptide massetolide A in biological control of Phytophthora infestans and in colonization of tomato plants by Pseudomonas fluorescens. New Phytol 175:731–742

Wang Q, Garrity GM, Tiedje JM, Cole JR (2007) Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Appl Environ Microb 73:5261–5267

Wang B, Yuan J, Zhang J, Shen Z, Zhang M, Li R, Ruan Y, Shen Q (2013) Effects of novel bioorganic fertilizer produced by *Bacillus amyloliquefaciens* W19 on antagonism of *Fusarium* wilt of banana. Biol Fertil Soils 49:435–446

Weller DM (1988) Biological control of soilborne plant pathogens in the rhizosphere with bacteria. Annu Rev Phytopathol 26:379–407

Wu TH, Chellemi DO, Graham JH, Martin KJ, Rosskopf EN (2008) Comparison of soil bacterial communities under diverse agricultural land management and crop production practices. Microb Ecol 55:293–310

Xu L, Huang B, Wu Y, Huang Y, Dong T (2011) The cost-benefit analysis for bananas diversity production in China Foc. zones. Am J Plant Sci 2:561–568

Xu M, Chen X, Qiu M, Zeng X, Xu J, Deng D, Sun G, Li X, Guo J (2012) Bar-coded pyrosequencing reveals the responses of PBDE-degrading microbial communities to electron donor amendments. PLoS ONE 7(1), e30439

Zhang F, Zhu Z, Yang X, Ran W, Shen Q (2013) *Trichoderma harzianum* T-E5 significantly affects cucumber root exudates and fungal community in the cucumber rhizosphere. Appl Soil Ecol 72:41–48

Zhao Q, Dong C, Yang X, Mei X, Ran W, Shen Q, Xu Y (2011) Biocontrol of *Fusarium* wilt disease for *Cucumis melo* melon using bio-organic fertilizer. Appl Soil Ecol 47:67–75

Zhao J, Zhang R, Xue C, Xun W, Sun L, Xu Y, Shen Q (2014) Pyrosequencing reveals contrasting soil bacterial diversity and community structure of two main winter wheat cropping systems in China. Microb Ecol 67:443–453