Soil bacterial and fungal communities of six bahiagrass cultivars

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ABSTRACT

Background. Cultivars of bahiagrass (*Paspalum notatum* Flüggé) are widely used for pasture in the Southeastern USA. Soil microbial communities are unexplored in bahiagrass and they may be cultivar-dependent, as previously proven for other grass species. Understanding the influence of cultivar selection on soil microbial communities is crucial as microbiome taxa have repeatedly been shown to be directly linked to plant performance.

Objectives. This study aimed to determine whether different bahiagrass cultivars interactively influence soil bacterial and fungal communities.

Methods. Six bahiagrass cultivars ('Argentine', 'Pensacola', 'Sand Mountain', 'Tifton 9', 'TifQuik', and 'UF-Riata') were grown in a randomized complete block design with four replicate plots of 4.6 × 1.8 m per cultivar in a Rhodic Kandiudults soil in Northwest Florida, USA. Three soil subsamples per replicate plot were randomly collected. Soil DNA was extracted and bacterial 16S ribosomal RNA and fungal ribosomal internal transcribed spacer 1 genes were amplified and sequenced with one Illumina Miseq Nano.

Results. The soil bacterial and fungal community across bahiagrass cultivars showed similarities with communities recovered from other grassland ecosystems. Few differences in community composition and diversity of soil bacteria among cultivars were detected; none were detected for soil fungi. The relative abundance of sequences assigned to nitrite-oxidizing *Nitrospira* was greater under 'Sand Mountain' than 'UF-Riata'. Indicator species analysis revealed that several bacterial and fungal indicators associated with either a single cultivar or a combination of cultivars are likely to be plant pathogens or antagonists.

Conclusions. Our results suggest a low impact of plant cultivar choice on the soil bacterial community composition, whereas the soil fungal community was unaffected. Shifts in the relative abundance of *Nitrospira* members in response to cultivar choice may have implications for soil N dynamics. The cultivars associated with presumptive plant pathogens or antagonists indicates that the ability of bahiagrass to control plant pathogens may be cultivar-dependent, however, physiological studies on plant-microbe interactions are required to confirm this presumption. We therefore suggest that future studies should explore the potential of different bahiagrass cultivars on plant pathogen control, particularly in sod-based crop rotation.

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INTRODUCTION

Bahiagrass (*Paspalum notatum* Flüggé), native to South America (*Burton, 1967*), is a widespread, warm-season perennial, commonly used as pasture in the Southeastern USA. Following its introduction into many countries worldwide, the sod-forming grass is also common in Australia and Japan (*Hirata, 2000*; *Wilson, 1987*) and has become naturalized in the USA. It was first introduced into the USA in 1913 (*Scott, 1920*) and is extensively cultivated on more than 1.5 million hectares in southeast USA, making it the most common and widely used perennial grass across southern states (*Newman, Vendramini & Blount, 2011*). Bahiagrass grows well in sandy, low fertile soils, requires low inputs, and it exhibits tolerance towards short-term drought and flooding events as well as continuous cattle stocking (*Gates, Quarin & Pedreira, 2004*; *Newman, Vendramini & Blount, 2011*). Low winter temperatures and aridity limit its geographic distribution (*Gates, Quarin & Pedreira, 2004*). 'Pensacola', 'Tifton 9', 'TifQuik', and 'UF-Riata' are among the most popular cultivars in the Southeastern USA. They exhibit differences in growth habit, cold tolerance, seasonal and total yield, seed production and grazing tolerance (*Newman, Vendramini & Blount, 2011*). Cultivars also can differ in their resistance to diseases (*Hancock et al., 2010*; *Trenholm, Cisar & Unruh, 2011*). Further, cultivar-specific nutrient use efficiencies may reduce nitrate leaching and fertilizer input costs (*Wiesler & Horst, 1993*; *Liu, Hull & Duff, 1997*; *Baligar, Fageria & He, 2001*). Therefore, cultivar choice is an important factor for the maintenance of soil health.

It is well established that plant community composition and diversity influences the belowground microbial community and vice-versa (*Berg, 2009*; *Berg & Smalla, 2009*; *Van der Heijden et al., 1998*; *Kourtev, Ehrenfeld & Häggblom, 2003*; *Kowalchuk et al., 2002*; *Lange et al., 2015*; *Reynolds et al., 2003*; *Wardle et al., 2004*; *Zak et al., 2003*). Beneficial plant-microbe interactions, such as mycorrhizal symbiosis or root colonization of plant growth-promoting rhizobacteria (PGPR) are known to enhance host plant growth (*Artursson, Finlay & Jansson, 2006*; *Lugtenberg & Kamilova, 2009*), pathogen resistance (*Azcón-Aguilar & Barea, 1997*; *Harrier & Watson, 2004*; *Van Loon, Bakker & Pieterse, 1998*; *Maherali & Klironomos, 2007*), and abiotic stress tolerance (*Evelin, Kapoor & Giri, 2009*; *Vurukonda et al., 2016*; *Wu, Zou & Xia, 2006*; *Yang, Kloepper & Ryu, 2009*). Whereby belowground, mycorrhiza symbionts depend on organic carbon supply via host roots (*Smith & Read, 2008*) and PGPR can be attracted via root exudates (*Badri & Jorge, 2009*; *Somers, Vanderleyden & Srinivasan, 2004*), creating a complex plant-microbe-soil feedback system (*Miki et al., 2010*). Emerging evidence shows that plant cultivars can be one of the factors affecting the composition of the rhizosphere microbiome (*Briones et al., 2002*; *Dalmastri et al., 1999*; *Diab El Arab, Vilich & Sikora, 2001*; *Germida & Siciliano, 2001*; *Schweitzer et al., 2008*). Different grass species have been shown to be capable of altering soil microbial communities, mainly due to differences in nutrient acquisition strategies

and rhizodeposits (*Bardgett et al., 1999*; *Grayston et al., 1998*; *Vandenkoornhuyse et al., 2003*). A few studies reported that rhizosphere bacterial populations vary across different grass cultivars (*Miller, Henken & Veen, 1989*; *Rodrigues et al., 2016*), whereas the potential effect of different grass cultivars on the composition of fungal communities remains widely unexplored. Identifying alterations of the soil microbiome by cultivar choice is of importance as specific microorganisms can have specific lifestyles, including mutualism, parasitism or involvement in diverse saprotrophic activities. These processes are directly linked to the fitness of the host plants and soil fertility.

Alterations of belowground microbial communities can have significant impact on plant performance. In several managed grassland ecosystems, Proteobacteria, Acidobacteria, Actinobacteria, and Bacteroidetes have been found to be the most abundant soil bacterial phyla (*Cao et al., 2017*; *Kaiser et al., 2016*; *Nacke et al., 2011*; *Rodrigues et al., 2016*; *Zhou et al., 2003*). Members of these phyla contribute to essential soil functions, such as biological nitrogen fixation (BNF) (*Baldani et al., 1997*). Further, beneficial rhizobacteria can stimulate plant growth via the production of plant hormones, suppress soil-borne plant pathogens, supply nutrients to plants and improve soil structure (*Berg, 2009*; *Hayat et al., 2010*; *Van der Heijden, Bardgett & Van Straalen, 2008*; *Weller et al., 2002*). Hence, PGPR such as *Arthrobacter*, *Azotobacter*, *Burkholderia*, and *Pseudomonas* species have been used to enhance agricultural production for decades (*Bhattacharyya & Jha, 2012*; *Vessey, 2003*). Besides bacteria, symbiotic associations with mycorrhizal fungi can improve plant resistance to pathogens (*Selosse, Baudoin, & Vandenkoornhuyse, 2004*; *Wehner et al., 2010*) as well as improve plant nutrition, particularly by enhancing plant phosphorus (P) acquisition (*Li et al., 2006*; *Smith, Mette Grønlund & Andrew Smith, 2011*; *Smith, Smith & Jakobsen, 2003*). Many arbuscular mycorrhizal (AM) fungi communities under grass have been shown to be dominated by the families Glomeraceae, Gigasporaceae and Acaulosporaceae (*Hiiesalu et al., 2014*; *Oehl et al., 2005*; *Xu et al., 2017*). In some grassland soils, the genus *Glomus* was identified as the most abundant AM fungi (*Gai et al., 2009*; *Wang et al., 2003*). *Glomus* is the largest genus of AM fungi described (*Schwarzott, Walker & Schüssler, 2001*). In association with peanut (*Arachis hypogaea*) and lettuce (*Lactuca sativa*) plants, *Glomus* spp. were demonstrated to promote plant growth, P and micronutrient uptake (*Krishna & Bagyaraj, 1984*) and increased drought tolerance (*Ruiz-Lozano, Azcon & Gomez, 1995*).

Using next generation amplicon sequencing, the aim of this study was to determine whether different bahiagrass cultivars interactively influence the belowground microbial community composition and diversity. To achieve this aim, we recovered bacterial 16S ribosomal RNA (16S rRNA) and fungal ribosomal internal transcribed spacer (ITS) 1 gene sequences from soil samples of six different bahiagrass cultivars grown in a randomized complete-block design. We hypothesized that bahiagrass cultivar choice affects the microbial community composition and diversity of both, soil bacteria and fungi. Given the significant role of soil microorganisms in soil nutrient cycling and plant nutrition, our research outcomes can provide insight into bahiagrass-associated soil bacterial and fungal communities, as well as the plant-microbe-soil feedback system among grass cultivars and better our understanding of the grassland ecosystem.

MATERIAL AND METHODS

Study site

The experimental site (30.8733 N, 85.1894 W, 33 m above sea level) is located in Northwest Florida (Jackson County), USA. The soil was characterized as a fine-loamy, kaolinitic, thermic Rhodic Kandiudults of the Orangeburg series (*National Cooperative Soil Survey U.S.A., 2019*). In June 2005, six different bahiagrass cultivars ('Argentine', 'Pensacola', 'Sand Mountain', 'Tifton 9', 'TifQuik', and 'UF-Riata') were established, in a randomized complete-block design, with four replicate plots of 4.6 × 1.8 m per cultivar. All plots were treated the same for harvesting procedures and fertilization rates. Bahiagrass cultivars were harvested five times to a 5-cm stubble height during the growing season (May to October), which was conducted at five-weeks intervals. The plots were grown under low-fertilizer inputs and received no nitrogen (N) fertilization for the duration of this study. From May to August 2015, the plots received 7.3 kg P ha^{-1}, 197.1 kg K ha^{-1}, 67.3 kg Mg ha^{-1}, and 141.2 kg S ha^{-1}. From April to August 2016, the plots received 29.4 kg P ha^{-1}, 239.9 kg K ha^{-1}, 33.6 kg Mg ha^{-1}, and 70.6 kg S ha^{-1}.

Soil characteristics were assessed prior to the planting in 2005. Five soil cores (Ø: 2.54 cm) of 0–15 cm depth were taken within each replicate plot to receive a total of 30 soil subsamples per block. One composite soil sample form each of the four blocks was analysed for soil pH (1:2, soil:water), Mehlich-1 extractable nutrients and calculated cation exchange capacity were determined by a commercial lab (Waters Agricultural Laboratories, Inc., Camilla, GA, USA). Soil properties are reported in Table S1.

Soil sampling and soil DNA extraction

Three randomly selected soil samples per replicate plot, resulting in twelve soil samples per cultivar, were taken in late April 2017 (mean temperature in April 2017: 22 °C [6–33 °C], sum of precipitation in April 2017: 51.8 mm [0.0–25.9 mm day^{-1}]). Soil cores (Ø: 2 cm) of 10 cm depth were stored at 4 °C during transportation to the laboratory (one hour). Upon arrival in the laboratory, soil samples were homogenized and sieved at ≤ 2 mm. Aliquots of each soil sample were transferred to 2 ml Eppendorf tubes, frozen in liquid N_2 for 3 min and subsequently stored at −80 °C until DNA extraction. Total soil DNA was extracted using Qiagen's DNeasy® PowerSoil® Kit (Qiagen Inc., CA, USA) following the manufacturer's instructions. Quality and quantity of the extracts were assessed using a spectrophotometer (NanoDrop (ND-ONE-W), ThermoFisher Scientific, Waltham, MA, USA).

Amplicon sequencing

To assess community compositions of soil bacteria and fungi, three-step PCRs targeting the bacterial V4 region of the 16S rRNA and fungal ITS1 genes were modified according to *Chen et al. (2018)*. Briefly, bacterial 16S rRNA and fungal ITS1 genes were amplified for 10 PCR cycles (first-step PCR) using primer pair 515F (5′-GTGCCAGCMGCCGCGGTAA-3′)/806R (5′-GACTACHVGGGTWTCTAAT-3′) and ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′)/ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′), respectively. Another 10 PCR cycles (2nd-step PCR) were used to add six

frameshifting primers as well as the sequencing primer. The frameshifting primers consisted of the respective primer pair used in the first-step PCR with frameshifting nucleotides to create sequence diversity in order to overcome the sequence bias within the initial bases and, thus, increase data yield (*Lundberg et al., 2013*). Finally, error tolerant barcodes were added running additional 10 PCR cycles (3rd-step PCR). Prior to pooling, 3rd-step PCR products were individually purified using bead-cleanup (AMPure XP, Beckman Instruments, Brea, CA, USA). Quality and quantity of the PCR products were assessed using a spectrophotometer (NanoDrop^{TM}). In addition, PCR products were screened on 1.7% (w/v) agarose gels to verify product size and quantity. The 144 barcoded PCR products were pooled and sequenced with one Illumina (Illumina Inc., San Diego, CA, USA) Miseq Nano (v2 250 bp, 500 Mb sequencing capacity) at Duke Center for Genomic and Computational Biology (GCB, Durham, NC, USA). Amplicon sequencing data have been deposited at NCBI Short Read Archive (SRP143584).

Amplicon sequencing data analysis

Sequence quality of obtained demultiplexed forward and reverse sequences was assessed by FastQC (*Andrews, 2010*). Forward primers were removed using cutadapt version 1.15 (*Martin, 2011*). Reverse sequences were not used due to low quality and merging with forward reads (*Nguyen et al., 2015*). The datasets were imported in QIIME2 verison 2018.11. Data were quality-filtered and chimeric sequences were removed employing DADA2 (*Callahan et al., 2016*). Forward reads truncated to 200 bp were processed for both bacterial and fungal datasets. The obtained 189,521 bacterial and 138,263 fungal quality-filtered reads were de novo assembled at 97% genetic identity using VSEARCH (*Rognes et al., 2016*). For taxonomic assignment, sequences were aligned to the Silva SSURef 132 NR (*Quast et al., 2013*) and UNITE version 7.2 database (*Kõljalg et al., 2013*) using BLAST+ (*Camacho et al., 2009*) in QIIME2 for 16S and ITS1, respectively. Singletons and non-bacterial and non-fungal reads were removed from the obtained operational taxonomic unit (OTU) tables. The OTU tables were rarefied to 1,200 for bacterial 16S rRNA and 600 randomly selected reads per sample for fungal ITS1 in QIIME2 (rarefaction curves are presented in Fig. S1).

Statistical analyses

Shannon-Wiener and Simpson's diversity indices, Chao1 richness estimate, and Simpson's evenness of samples from rarefied OTU tables were calculated using the 'diversity'-function in the R package 'vegan' version 2.4-5 (*Oksanen, 2017*). Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices was conducted using the 'metaMDS'-function in 'vegan'. Significant differences in alpha diversity metrics (Shannon-Wiener and Simpson's diversity indices, Chao1 richness estimate, and Simpson's evenness) were tested using Kruskal-Wallis test with multiple comparison extension ('kruskalmc'-function in the 'pgirmess' R package version 1.6.9 (*Giraudoux et al., 2018*). We further tested for significant differences in the relative abundance of taxonomic groups at all taxonomic levels (phylum to species) using one-way ANOVA with Tukey's HSD test or Kruskal-Wallis test with multiple comparison extension as described above. Indicator

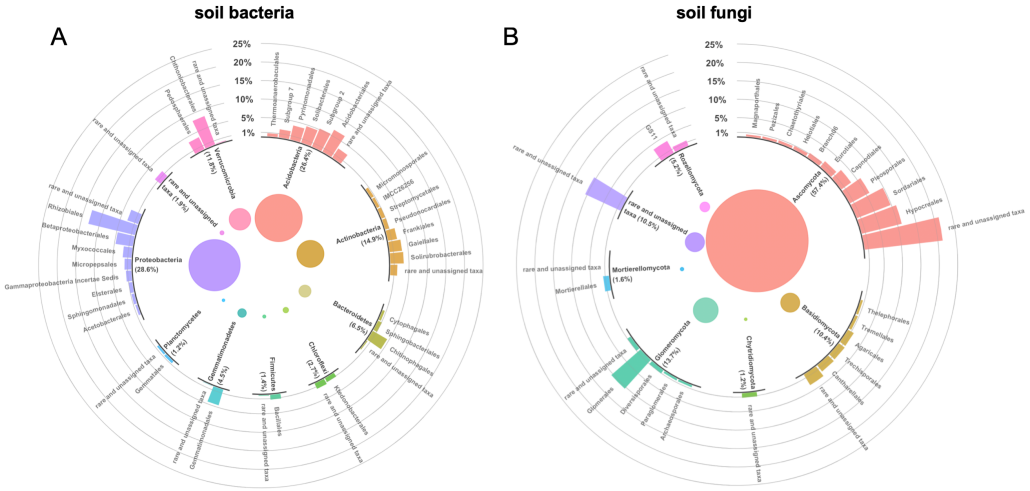

Figure 1 (A) Soil bacterial and (B) fungal community composition across plots of six different bahiagrass (*Paspalum notatum* Flüggé) cultivars ($n = 72$) in a Rhodic Kandiudults soil in Northwest Florida, USA. Rare (<0.5% relative abundance) phyla and orders were grouped with unassigned taxa.
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species of individual plant cultivars as well as a combination of cultivars were identified using the 'multipatt'-function using 999 permutations in the 'indicspecies' R package version 1.7.6 (*De Caceres, 2013*).

Differences in community composition among cultivars were tested using permutational multivariate analysis of variance (PERMANOVA) and complementary test for homogeneity of dispersions (PERMDISP) using 9,999 permutations employing the 'beta-group-significance'-function in QIIME2 version 2018.11. Results for both PERMANOVA and PERMDISP were corrected for multiple comparison using Benjamini–Hochberg correction. Complementary, we performed Analysis of similarities (ANOSIM) using 9,999 permutations using the same function as for PERMANOVA and PERMDISP, yielding in similar results. Here, we report the results from PERMANOVA and PERMDISP. Test results with $p < 0.05$ were considered statistically significant. All statistical analyses were executed in R version 3.4.3 (*R Core Team, 2017*).

RESULTS

Microbial community composition across six bahiagrass cultivars

The most abundant soil bacterial phyla were Proteobacteria (28.6 ± 8.5%), Acidobacteria (26.4 ± 10.2%), Actinobacteria (14.9 ± 3.3%), and Verrucomicrobia (11.8 ± 9.0%) (Fig. 1A). The Proteobacteria were divided into Alpha- (18.5 ± 8.1%), Delta-(3.0 ± 1.2%), and Gammaproteobacteria (7.1 ± 1.4%). Rhizobiales (12.9 ± 7.9%), Chthoniobacterales (8.2 ± 8.9%), Acidobacterales (6.7 ± 4.3%), and 'Subgroup 2' (5.3 ± 8.5%) were the dominant bacterial orders in soil (Fig. 1A). Sequences that matched closest with Candidatus *Udaeobacter* (8.2 ± 6.7%), *Bradyrhizobium* (4.7 ± 7.0%), and Candidatus *Solibacter* (2.7 ± 1.6%) were the most abundant in occurrence bacterial genera across cultivars.

Ascomycota (54.7 ± 13.8%), Glomeromycota (13.7 ± 7.5%), Basidiomycota (10.4 ± 8.6%), and Rozellomycota (9.8 ± 7.0%) were the most abundant fungal phyla (Fig. 1B). On class level, the fungal communities were dominated by Sordariomycetes (28.9 ± 14.0%), Glomeromycetes (11.7 ± 7.0%), Dothideomycetes (9.4 ± 9.2%), and Agaricomycetes (8.4 ± 8.6%). The most dominant fungal orders were Hypocreales (11.2 ± 9.0%), Sordariales (10.5 ± 7.0%), Glomerales (9.8 ± 10.2%), and Pleosporales (6.0 ± 5.0%) (Fig. 1B). Sequences that matched closest with *Penicillium* (1.9 ± 1.9%), *Fusarium* (1.8 ± 1.2%), and *Mortierella* (1.4 ± 1.7%) were the dominant fungal genera.

Soil microbial diversity under different bahiagrass cultivars

To understand whether bahiagrass cultivar is among the factors shaping the community of soil microorganisms, the community composition and diversity of soil microorganisms across different cultivars was compared. Differences in the soil bacterial community composition between Argentine and Sand Mountain ($p = 0.022$) as well as Argentine and TifQuik were detected ($p = 0.022$) (Table S2). Soil fungal community composition did not differ among cultivars (Table S2), which is demonstrated by the clustering of the cultivars in the NMDS (Fig. 2B).

The different cultivars did not differ in their bacterial and fungal diversity based on the Shannon-Wiener diversity index; however, using Simpson's diversity index, a greater diversity of bacteria in soil of UF-Riata compared to TifQuik was observed ($p = 0.015$) (Fig. 2C). No differences in bacterial and fungal richness were observed among cultivars, and Simpson's evenness revealed lower bacterial species evenness in soil under TifQuik than Argentine ($p = 0.023$), Pensacola ($p = 0.002$), and UF-Riata ($p < 0.001$) (Fig. 2C).

Shifts of relative abundance and indicator species in response to different bahiagrass cultivars

We detected only one relative abundance shift of the bacterial and none of the fungal taxonomic groups among cultivars. The shift was found for the bacterial genus *Nitrospira*, where Sand Mountain was showing greater relative abundance than UF-Riata ($p = 0.049$) (Fig. 3A).

Out of 425 bacterial OTUs, there were 13 indicator species for individual cultivars as well as a combination of cultivars from which the majority of indicators (8 out of 13) were identified as Proteobacteria. Sand Mountain and TifQuik were the only individual cultivars that harboured distinct indicator species from the other cultivars in this study. The remaining indicators species were assigned to a combination of cultivars (Table S3). An OTU that matched closest to *Pajaroellobacter* (Deltaproteobacteria) and one that was assigned to *Bauldia* (Alphaproteobacteria) were associated with Sand Mountain ($p \leq 0.048$) (Table S3). For the cultivar TifQuik, an OTU of the order '54-9' (Anaerolineae) was identified as an indicator species ($p = 0.019$) (Table S3). Further, an OTU matched closest to *Haliangium* (Deltaproteobacteria) was characterised as an indicator species for Pensacola and Tifton 9 ($p = 0.008$) (Table S3). The presence of an unassigned member of the family Nitrosomonadaceae (Gammaproteobacteria) was identified as an indicator for all cultivars but Argentine ($p = 0.017$) (Table S3).

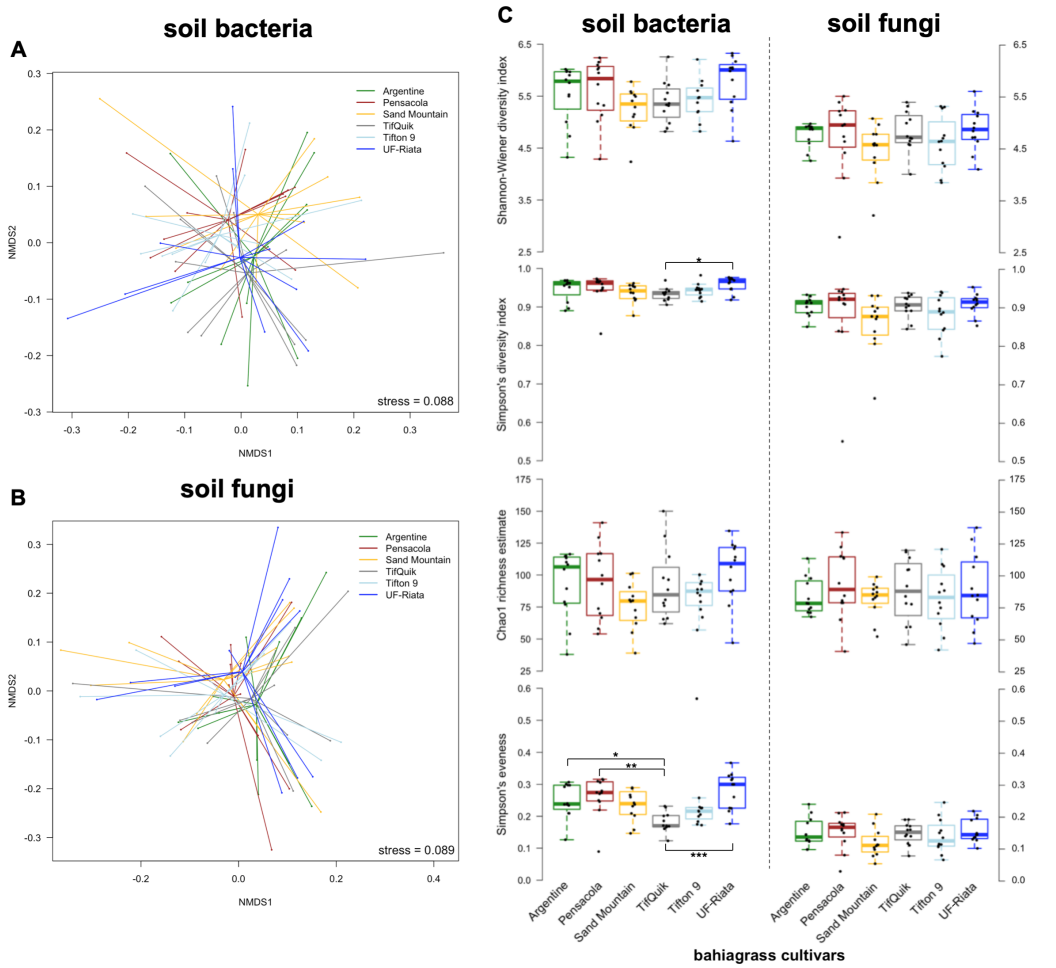

Figure 2 Microbial community composition and diversity in soil of six different bahiagrass (*Paspalum notatum* Flüggé) cultivars ($n = 12$ for each cultivar) in a Rhodic Kandiudults soil in Northwest Florida, USA. (A) Non-metric multidimensional scaling ordination (NMDS) of Bray-Curtis dissimilarity matrices of the soil bacterial and (B) fungal community, and (C) diversity, richness, and evenness metrics of soil bacterial and fungal communities. Black dots represent individual data points. Brackets indicate statistically significant differences among cultivars (Kruskal-Wallis test with multiple comparison extension at $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$).

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Of a total of 180 fungal OTUs, six indicator species were detected (Table S4). One OTU of the family Ceratobasidiaceae (Agaricomycetes) was characterized as an indicator for Pensacola, Sand Mountain, and Tifton 9 ($p = 0.016$) (Table S4). Sand Mountain, TifQuik, Tifton 9, and UF-Riata were characterized by a fungal OTU assigned to the family Orbiliaceae ($p = 0.040$) (Table S4).

DISCUSSION

Soil bacterial communities across bahiagrass cultivars

The soil bacterial communities across managed bahiagrass cultivars exhibited parallels to the communities of diverse grassland ecosystems at phylum and class level. For example,

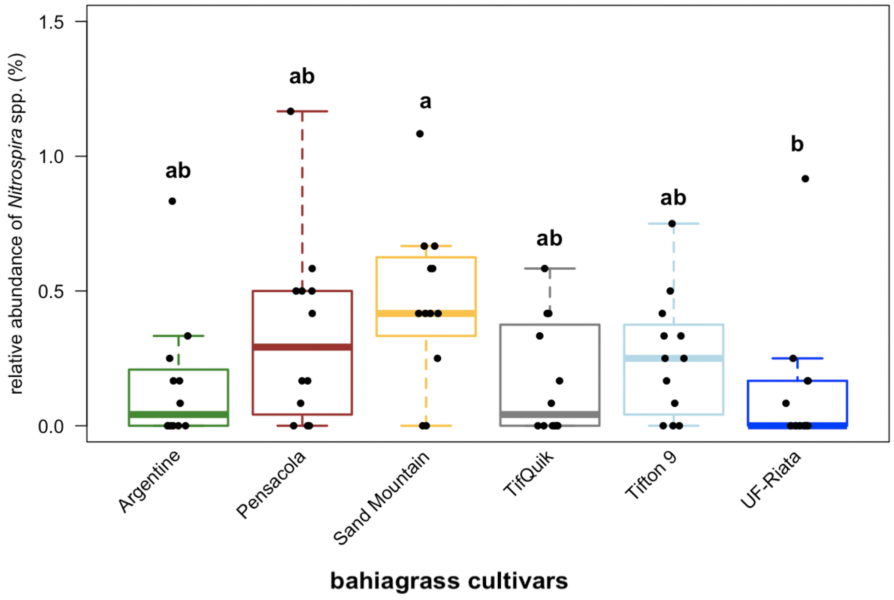

Figure 3 **Relative abundance of *Nitrospira*. in soil of six different bahiagrass (*Paspalum notatum* Flüggé) cultivars ($n = 12$ for each cultivar) in a Rhodic Kandiudults soil in Northwest Florida, USA.** Black dots represent individual data points. Different lowercase letters indicate statistically significant differences among cultivars (Kruskal-Wallis test with multiple comparison extension at $p < 0.05$).
Full-size DOI: 10.7717/peerj.7014/fig-3

the top three dominant soil bacterial phyla across all bahiagrass plots (Proteobacteria, Acidobacteria, and Actinobacteria) as well as the dominance of the Alpha-, Delta-, and Gammaproteobacteria were also reported for managed grassland soils (*Cao et al., 2017*; *Nacke et al., 2011*; *Rodrigues et al., 2016*; *Zhou et al., 2003*). Further, the greater relative abundance of the phyla Acidobacteria and Actinobacteria agrees with other studies investigating bacterial communities in grassland soils (*Kaiser et al., 2016*; *Nacke et al., 2011*; *Rodrigues et al., 2016*; *Will et al., 2010*).

The most abundant bacterial genus that was taxonomically assigned across cultivars of bahiagrass, Candidatus *Udaeobacter*, is ubiquitous in soils and frequently recovered using 16S rRNA gene sequencing approaches. Recently, *Brewer et al. (2016)* reported that an affiliate of this genus, Candidatus *Udaeobacter copiosus*, can account for almost one third of the soil bacterial taxa in grasslands. Further, Candidatus *Udaeobacter copiosus* has shown dominance in soil samples even across geographic distance (*Brewer et al., 2016*). Despite its great relative abundance in soils worldwide, the ecology and physiology of members of the genus Candidatus *Udaeobacter* largely remain unknown.

Our second most abundant soil bacterial genus (*Bradyrhizobium*) that matched our sequences was previously found as one of the most prominent genera in other grassland ecosystems (*Brewer et al., 2016*; *McCaig, Glover & Prosser, 1999*; *Thomson et al., 2010*). Many *Bradyrhizobium* species have the ability to denitrify (*Bedmar, Robles & Delgado, 2005*; *Fernández et al., 2008*; *Kaneko et al., 2002*; *Mesa, Göttfert & Bedmar, 2001*) and are proposed to play a key role in denitrification (*Jones et al., 2016*). Moreover, several

Bradyrhizobium affiliates are capable of fixing atmospheric N_2 and are considered to contribute significantly to BNF in soils (*Zahran, 1999*). The abundance of *Bradyrhizobium*, however, cannot serve as an indicator of their N_2 fixation rates as shown in a recent study on native switchgrass (*Panicum virgatum*) (*Bahulikar et al., 2014*). Thus, although a genetic potential for denitrification and BNF is given by our second most dominant soil bacterial genus, its contribution to N cycling in soil of bahiagrass remains unclear and requires further investigations on functional level.

In line with the other dominant genera that we taxonomically assigned, the genus Candidatus *Solibacter*, our third most abundant genus, has been reported as one of the top genera recovered from grassland soils (*Kaiser et al., 2016*). Even for the most frequently investigated affiliate of the genus, Candidatus *Solibacter usitatus*, detailed ecological and physiological information is still lacking (*Dedysh et al., 2017*; *Ward et al., 2009*).

Soil fungal communities across bahiagrass cultivars

In line with previous results from grassland ecosystems (*Barnard, Osborne & Firestone, 2013*; *Chen et al., 2017*:201; *Porras-Alfaro & Bayman, 2011*; *Tedersoo et al., 2014*; *Yang et al., 2017*), sequences assigned to Ascomycota numerically dominated over all other fungal phyla across cultivars. The dominant fungal classes in our bahiagrass plots (Sordariomycetes, Glomeromycetes, Dothideomycetes, and Agaricomycetes) were similar to those found in Californian grassland soils (*Barnard, Osborne & Firestone, 2013*).

Many species of our most abundant taxonomically assigned fungal genus across cultivars, *Penicillium*, have been identified as plant growth-promoting fungi for several plants including grasses (*Khan et al., 2008*; *Wakelin et al., 2004*; *Whitelaw, Harden & Bender, 1997*). A well reported mechanism of plant growth promotion by *Penicillium* spp. is their ability to solubilize P for plant nutrition in soil (*Asea, Kucey & Stewart, 1988*; *Kucey, 1987*; *Wakelin et al., 2004*). We found that the potentially phytopathogenic genus *Fusarium* was assigned as the second most abundant genus across all plots. *Fusarium* spp. are cosmopolitans that are present in all types of ecosystems (*Summerell et al., 2010*) and were reported to be one of the most abundant soil fungal taxa in some grassland ecosystems (*Khidir et al., 2010*; *Orgiazzi et al., 2012*; *Warcup, 1951*; *Yang et al., 2017*). *Fusarium* diseases are, except under rare conditions, considered as not serious for bahiagrass under field conditions (*Singh, 2009*). Besides *Penicillium* and *Fusarium*, sequences assigned to the genus *Mortierella* were dominant and have also been shown to be highly abundant in grassland soils (*Warcup, 1951*; *Yang et al., 2017*). Members of the genus *Mortierella* are a diverse, ubiquitous and abundant group of filamentous fungi in soils that exhibit a saprophytic lifestyle (*Uehling et al., 2017*; *Wagner et al., 2013*). Additionally, some species were recently described as root endophytes (*Bonito et al., 2016*; *Johnson et al., 2019*). There is evidence that several *Mortierella* species can promote the growth of certain plant species whereby for some species, similar to *Penicillium*, one of the identified mechanisms for plant growth promotion is their ability to solubilize P for plant uptake (*Osorio & Habte, 2001*; *Osorio & Habte, 2013*; *Osorio & Habte, 2014*; *Sharma et al., 2013*; *Zhang et al., 2011*).

Soil bacteria and fungi under different bahiagrass cultivars

Numerous studies have shown that plant cultivars or varieties can affect the composition of the associated soil rhizosphere bacterial and fungal communities (*Bell et al., 2014*; *Briones et al., 2002*; *Dalmastri et al., 1999*; *Diab El Arab, Vilich & Sikora, 2001*; *Germida & Siciliano, 2001*; *Jie, Liu & Cai, 2013*; *Schweitzer et al., 2008*). Different grass cultivars can exhibit dissimilar nutrient requirements (*Ashworth et al., 2017*; *Oliveira et al., 2017*) as well as root exudate quantities and qualities (*Christiansen-Weniger, Groneman & Van Veen, 1992*; *Guo, McCulley & McNear, 2015*), which are likely to affect populations of root-associated microorganisms. The bahiagrass cultivars differed in productivity, stand establishment and growth rate, and temperature sensitivity (*Chambliss & Sollenberger, 1991*; *Newman, Vendramini & Blount, 2011*). Thus, considering the holistic approach of plant-microbe-soil as a feedback system (*Miki et al., 2010*), it is likely that different bahiagrass cultivars affect the rhizosphere microbiome and alter plant-microbe-soil traits. In our study, differences in microbial community composition in response to cultivar choice were only detected for bacterial communities. It should be noted that our soil samples were a mixture of rhizosphere and bulk soil, which may have contributed to the low number of detected differences in the composition and diversity of soil microbial communities among cultivars. Soil microbial community functional diversification is thought to be crucial for soil microbiome stability and resilience (*Griffiths & Philippot, 2013*; *Shade et al., 2012*). Therefore, the comparingly low bacterial alpha diversity (Simpson's index) and evenness (Simpson's evenness) in TifQuik soil (Fig. 2C), may signal a decreased potential of the soil bacterial community to counter perturbations.

Differences in community composition among cultivars were limited to bacterial communities among Argentine and Sand Mountain and Argentine and TifQuik. Cultivar choice further affected relative abundance of the cosmopolitan genus *Nitrospira* (Fig. 3). *Nitrospira* affiliates are present in a wide range of habitats, including deep sea sediments (*Nunoura et al., 2015*), cold deserts (*Gupta et al., 2015*), and tropical sponges (*Sharp et al., 2007*). Traditionally, members of *Nitrospira* are described as nitrite-oxidizing bacteria, performing the second oxidation-step in nitrification. Recently, however, *Daims et al. (2015)* reported complete nitrification by a member of the genus *Nitrospira*, which completely changes our understanding of ammonia-oxidizing and nitrite-oxidizing bacteria. Apart from their place in the nitrification pathway, the increased relative abundance of *Nitrospira* under Sand Mountain compared to UF-Riata (Fig. 3) may indicate a greater potential for nitrite oxidation activity in soil of Sand Mountain. In 2014 and 2015, *Dubeux et al. (2017)* determined the bahiagrass yield and crude protein content of all six bahiagrass cultivars at our experimental site. The yield of Sand Mountain was among the greatest of all six cultivars and out-yielded Argentine. Although no statistically significant differences in crude protein content were detected among cultivars, it is worth mentioning that Sand Mountain showed the greatest mean crude protein content (*Dubeux et al., 2017*).

Wedin & Tilman (1990) reported a close relationship between soil-N cycling and the choice of perennial grass species. Several studies showed that certain grass species can suppress nitrification (*Ishikawa et al., 2003*; *Lata et al., 2004*; *O'Sullivan et al., 2016*;

Subbarao et al., 2009). In contrast, *Hawkes et al. (2005)* demonstrated that invasive grass species can increase nitrification rates and the abundance of ammonia-oxidizing bacteria in soil of Californian grassland. Studies that explored the role of grass root exudates on nitrification mainly focused on nitrification inhibition as a strategy for reduced nitrate leaching from soil. Numerous studies reported nitrification inhibitors in root exudates of grasses (*Subbarao et al., 2006*; *Subbarao et al., 2009*; *Sun et al., 2016*; *Zakir et al., 2008*). The composition of grass root-exudates has been shown to be affect by both cultivar and fungal endophytes (*Guo, McCulley & McNear, 2015*). It remains unclear whether certain bahiagrass cultivars affect nitrification rates. However, we speculate that some cultivars may promote or less supress nitrifying soil microorganisms to increase N availability, particularly in the absence of N fertilization like at our experimental site.

Sand Mountain further harboured two indicator species, one OTU anchored in the genus *Pajaroellobacter* and the other in the genus *Bauldia* (Table S3). The genus *Pajaroellobacter* is not well characterized, except for *Pajaroellobacter abortibovis*, the etiologic agent of epizootic bovine abortion in cattle, which is a vector transmitted disease by the tick *Ornithodoros coriaceus* (*Brooks et al., 2016*; *King et al., 2005*). Likewise, the genus *Bauldia* is largely unexplored.

Sequences assigned to the genus *Haliangium* was found characteristic for the cultivars Pensacola and Tifton 9 (Table S3). *Haliangium* spp. have been recovered from soil samples before, even with great geographic distance among samples (*Ding et al., 2014*; *Fulthorpe et al., 2008*). Some members of *Haliangium* have the capability to produce the antifungal metabolite haliangicin which can supress the growth of a broad range of fungi (*Fudou, Iizuka & Yamanaka, 2001*; *Kundim et al., 2003*). There is no application of *Haliangium* in plant protection yet, however, the potential of myxobacteria to produce unique secondary metabolites has been recognized (*Reichenbach & Höfle, 1993*; *Wenzel & Müller, 2009*).

For all cultivars but Argentine, an OTU of the abundant bacterial family Nitrosomonadaceae was assigned as an indicator species (Table S1). They are characterized as lithoautotrophic of ammonia-oxidizing bacteria and harbour the well-characterized genera *Nitrosomonas* and *Nitrosospira*. In view if this result and the relative abundances of *Nitrospira*, we suggest that the dynamics of soil-N cycling under different bahiagrass cultivars should be further investigated.

Half of the cultivars (Pensacola, Sand Mountain, and Tifton 9) harboured a sequence assigned to a member of the Ceratobasidiaceae as an indicator species (Table S4). Genera of this fungal family include economically relevant phytopathogens like *Rhizoctonia*, which cause, for example, 'brown patch' disease on turfgrasses (*Oniki et al., 1986*). In rotation systems, bahiagrass has shown to reduce *Rhizoctonia* population densities in soil and associated diseases on peanuts (*Johnson et al., 1999*), and vegetables (cucumber (*Cucumis sativus* 'Comet') and snap bean (*Phaseolus vulgaris* 'Strike')) (*Sumner et al., 1999*). The two tested bahiagrass cultivars in the above-mentioned studies on peanuts and vegetables were Pensacola and Tifton 9, respectively. Since Pensacola, Sand Mountain, and Tifton 9 were characterized by an OTU assigned to a member of the Ceratobasidiaceae, our bahiagrass cultivars may differ in their ability to suppress *Rhizoctonia* population in soils. Therefore, it may be valuable to screen bahiagrass cultivars for disease suppression when used in

sod-based crop rotations (i.e., 1 to 8 years of peanuts or vegetables rotated with 2 to 10 years of bahiagrass).

An OTU assigned to the widespread family Orbiliaceae was identified as an indicator species of the cultivars Sand Mountain, TifQuik, Tifton 9, and UF-Riata (Table S4). Several members of this family are carnivorous fungi which trap nematodes in soils (*Pfister, 1997*; *Rubner, 1996*). The underlying mechanisms of biocontrol of nematodes by microorganisms are well described (*Li et al., 2015*). Rotations of bahiagrass with peanuts, soybean (*Glycine max*), or vegetables have shown the potential to increase nematode control (*Rodriguez-Kabana et al., 1988*; *Rodriguez-Kabana et al., 1989*; *Sumner et al., 1999*). However, there is a lack of studies comparing the performance of different bahiagrass cultivars on nematode control. Based on our molecular results, we speculate that bahiagrass cultivar screening may improve nematode biocontrol.

CONCLUSIONS

We detected a few differences in community composition and diversity of soil bacteria among bahiagrass cultivars, suggesting a moderate impact of cultivar choice on the soil bacterial community. Further, cultivar choice affected the relative abundance of sequences assigned to members of the nitrite-oxidizing bacterial genus *Nitrospira* with possible implications for soil-N dynamics. In contrast, soil fungal composition and diversity was not altered by the different cultivars. Several bacterial and fungal indicator species assigned to either a single cultivar or a combination of cultivars were presumptive plant pathogens or antagonists. In view of this, we suggest future work that explores the potential of bahiagrass cultivars to control plant pathogens.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Lukas Beule conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Ko-Hsuan Chen conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper.
- Chih-Ming Hsu conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools.
- Cheryl Mackowiak authored or reviewed drafts of the paper, approved the final draft.
- Jose C.B. Dubeux Jr. conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper.
- Ann Blount conceived and designed the experiments, authored or reviewed drafts of the paper.
- Hui-Ling Liao conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.

Data Availability

The following information was supplied regarding data availability:

Amplicon sequencing data are available at NCBI Short Read Archive (SRP143584). Available at https://www.ncbi.nlm.nih.gov/Traces/study/?acc=PRJNA454081

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REFERENCES

Andrews S. 2010. FastQC: a quality control tool for high throughput sequence data. *Available at http://www.bioinformatics.babraham.ac.uk/projects/fastqc/* (accessed on 01 February 2019).

Artursson V, Finlay RD, Jansson JK. 2006. Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. *Environmental Microbiology* **8(1)**:1–10 DOI 10.1111/j.1462-2920.2005.00942.x.

Asea PEA, Kucey RMN, Stewart JWB. 1988. Inorganic phosphate solubilization by two penicillium species in solution culture and soil. *Soil Biology and Biochemistry* **20(4)**:459–464 DOI 10.1016/0038-0717(88)90058-2.

Ashworth AJ, Allen FL, Bacon JL, Sams CE, Hart WE, Grant JF, Moore PA, Pote DH. 2017. Switchgrass cultivar, yield, and nutrient removal responses to harvest timing. *Agronomy Journal* **109(6)**:2598–2605 DOI 10.2134/agronj2017.01.0018.

Azcón-Aguilar C, Barea JM. 1997. arbuscular mycorrhizas and biological control of soil-borne plant pathogens—an overview of the mechanisms involved. *Mycorrhiza* **6(6)**:457–464 DOI 10.1007/s005720050147.

Badri DV, Vivanco JM. 2009. Regulation and function of root exudates. *Plant, Cell & Environment* **32(6)**:666–681 DOI 10.1111/j.1365-3040.2009.01926.x.

Bahulikar RA, Torres-Jerez I, Worley E, Craven K, Udvardi MK. 2014. Diversity of nitrogen-fixing bacteria associated with switchgrass in the native Tallgrass Prairie of Northern Oklahoma. *Applied and Environmental Microbiology* **80(18)**:5636–5643 DOI 10.1128/AEM.02091-14.

Baldani JI, Caruso L, Baldani VLD, Goi SR, Döbereiner J. 1997. Recent advances in BNF with non-legume plants. *Soil Biology and Biochemistry* **29(5–6)**:911–922 DOI 10.1016/S0038-0717(96)00218-0.

Baligar VC, Fageria NK, He ZL. 2001. Nutrient use efficiency in plants. *Communications in Soil Science and Plant Analysis* **32(7–8)**:921–950 DOI 10.1081/CSS-100104098.

Bardgett RD, Mawdsley JL, Edwards S, Hobbs PJ, Rodwell JS, Davies WJ. 1999. Plant species and nitrogen effects on soil biological properties of temperate upland grasslands. *Functional Ecology* **13(5)**:650–660 DOI 10.1046/j.1365-2435.1999.00362.x.

Barnard RL, Osborne CA, Firestone MK. 2013. responses of soil bacterial and fungal communities to extreme desiccation and rewetting. *The ISME Journal* **7(11)**:2229–2241 DOI 10.1038/ismej.2013.104.

Bedmar EJ, Robles EF, Delgado MJ. 2005. The complete denitrification pathway of the symbiotic, nitrogen-fixing bacterium bradyrhizobium japonicum. *Biochemical Society Transactions* **33(pt 1)**:141–144 DOI 10.1042/BST0330141.

Bell TH, El-Din Hassan S, Lauron-Moreau A, Al-Otaibi F, Hijri M, Yergeau E, St-Arnaud M. 2014. Linkage between bacterial and fungal rhizosphere communities in hydrocarbon-contaminated soils is related to plant phylogeny. *The ISME Journal* **8(2)**:331–343 DOI 10.1038/ismej.2013.149.

Berg G. 2009. Plant-microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. *Applied Microbiology and Biotechnology* **84(1)**:11–18 DOI 10.1007/s00253-009-2092-7.

Berg G, Smalla K. 2009. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology* **68(1)**:1–13 DOI 10.1111/j.1574-6941.2009.00654.x.

Bhattacharyya PN, Jha DK. 2012. Plant Growth-Promoting Rhizobacteria (PGPR): emergence in agriculture. *World Journal of Microbiology and Biotechnology* **28(4)**:1327–1350 DOI 10.1007/s11274-011-0979-9.

Bonito G, Hameed K, Ventura R, Krishnan J, Schadt CW, Vilgalys R. 2016. Isolating a functionally relevant guild of fungi from the root microbiome of populus. *Fungal Ecology Complete* **22**:35–42.

Brewer TE, Handley KM, Carini P, Gilbert JA, Fierer N. 2016. Genome reduction in an abundant and ubiquitous soil bacterium. Candidatus Udaeobacter Copiosus. *Nature Microbiology* **2(2)**:Article 16198 DOI 10.1038/nmicrobiol.2016.198.

Briones AM, Okabe S, Umemiya Y, Ramsing N-B, Reichardt W, Okuyama H. 2002. Influence of different cultivars on populations of ammonia-oxidizing bacteria in the

root environment of rice. *Applied and Environmental Microbiology* **68(6)**:3067–3075 DOI 10.1128/AEM.68.6.3067-3075.2002.

Brooks RS, Blanchard MT, Clothier KA, Fish S, Anderson ML, Stott JL. 2016. Characterization of pajaroellobacter abortibovis, the etiologic agent of epizootic bovine abortion. *Veterinary Microbiology* **192**:73–80 DOI 10.1016/j.vetmic.2016.07.001.

Burton GW. 1967. A search for the origin of Pensacola Bahia Grass. *Economic Botany* **21(4)**:379–382 DOI 10.1007/BF02863165.

Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP. 2016. DADA2: high-resolution sample inference from illumina amplicon data. *Nature Methods* **13(7)**:581–583 DOI 10.1038/nmeth.3869.

Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL. 2009. BLAST+: architecture and applications. *BMC Bioinformatics* **10**:421.

Cao C, Zhang Y, Qian W, Liang C, Wang C, Tao S. 2017. Land-use changes influence soil bacterial communities in a Meadow Grassland in Northeast China. *Solid Earth* **8**:1119–1129 DOI 10.5194/se-8-1119-2017.

Chambliss CG, Sollenberger L. 1991. Bahiagrass: the foundation of cow-calf nutrition in Florida. In: *Proceedings of the 40th Annual Beef Cattle Short Course. Gainesville, Florida: IFAS, University of Florida, Gainesville, Florida*. 74–80.

Chen K-H, Liao H-L, Elizabeth Arnold A, Bonito G, Lutzoni F. 2018. RNA-based analyses reveal fungal communities structured by a senescence gradient in the moss dicranum scoparium and the presence of putative multi-trophic fungi. *The New Phytologist* **218(4)**:1597–1611 DOI 10.1111/nph.15092.

Chen Y-L, Xu T-L, Veresoglou SD, Hu H-W, Hao Z-P, Hu Y-J, Liu L, Deng Y, Rillig MC, Chen B-D. 2017. Plant diversity represents the prevalent determinant of soil fungal community structure across temperate grasslands in Northern China. *Soil Biology and Biochemistry* **110**:12–21 DOI 10.1016/j.soilbio.2017.02.015.

Christiansen-Weniger C, Groneman AF, Van Veen JA. 1992. Associative N2 fixation and root exudation of organic acids from wheat cultivars of different aluminium tolerance. *Plant and Soil* **139(2)**:167–174 DOI 10.1007/BF00009307.

Daims H, Lebedeva EV, Pjevac P, Han P, Herbold C, Albertsen M, Jehmlich N, Palatinszky M, Vierheilig J, Bulaev A, Kirkegaard RH, Von Bergen M, Rattei T, Bendinger B, Nielsen PH, Wagner M. 2015. Complete nitrification by nitrospira bacteria. *Nature* **528(7583)**:504–509 DOI 10.1038/nature16461.

Dalmastri C, Chiarini L, Cantale C, Bevivino A, Tabacchioni S. 1999. Soil type and maize cultivar affect the genetic diversity of maize root–associated burkholderia cepacia populations. *Microbial Ecology* **38(3)**:273–284 DOI 10.1007/s002489900177.

De Caceres M. 2013. How to use the indicspecies package (ver. 1.7.1). *Available at ftp://12861.111.11/pub/cran/web/packages/indicspecies/vignettes/indicspeciestutorial.pdf* (accessed on 01 February 2019).

Dedysh SN, Kulichevskaya IS, Huber KJ, Overmann J. 2017. Defining the taxonomic status of described subdivision 3 acidobacteria: proposal of bryobacteraceae fam. nov. *International Journal of Systematic and Evolutionary Microbiology* **67(2)**:498–501 DOI 10.1099/ijsem.0.001687.

Diab El Arab HG, Vilich V, Sikora RA. 2001. The use of phospholipid fatty acids (PL-FA) in the determination of Rhizosphere Specific Microbial Communities (RSMC) of two wheat cultivars. *Plant and Soil* **228(2)**:291–297 DOI 10.1023/A:1004814229653.

Ding G-C, Radl V, Schloter-Hai B, Jechalke S, Heuer H, Smalla K, Schloter M. 2014. Dynamics of soil bacterial communities in response to repeated application of manure containing sulfadiazine. *PLOS ONE* **9(3)**:e92958 DOI 10.1371/journal.pone.0092958.

Dubeux J, Santos ERS, Garcia-Jimenez L, Jaramillo D, Blount AR, Mackowiak C. 2017. Bahiagrass performance under low soil nitrogen. 2017 Florida Beef Research Report. Department of Animal Sciences, University of Florida. 153–156.

Evelin H, Kapoor R, Giri B. 2009. Arbuscular mycorrhizal fungi in alleviation of salt stress: a review. *Annals of Botany* **104(7)**:1263–1280 DOI 10.1093/aob/mcp251.

Fernández LA, Beatriz Perotti E, Antonio Sagardoy M, Anahí Gómez M. 2008. Denitrification activity of bradyrhizobium sp. isolated from argentine soybean cultivated soils. *World Journal of Microbiology & Biotechnology* **24(11)**:2577–2585 DOI 10.1007/s11274-008-9828-x.

Fudou R, Iizuka T, Yamanaka S. 2001. Haliangicin, a novel antifungal metabolite produced by a marine myxobacterium. 1. fermentation and biological characteristics. *The Journal of Antibiotics* **54(2)**:149–152 DOI 10.7164/antibiotics.54.149.

Fulthorpe RR, Roesch LFW, Riva A, Triplett EW. 2008. Distantly sampled soils carry few species in common. *The ISME Journal* **2(9)**:901–910 DOI 10.1038/ismej.2008.55.

Gai JP, Christie P, Cai XB, Fan JQ, Zhang JL, Feng G, Li XL. 2009. Occurrence and distribution of arbuscular mycorrhizal fungal species in three types of grassland community of the tibetan plateau. *Ecological Research* **6(24)**:1345–1350.

Gates RN, Quarin CL, Pedreira CGS. 2004. Bahiagrass. In: Moser LE, Burson BL, Sollenberger LE, eds. *Warm-season (C4) grasses*. Wisconsin: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, 651–680.

Germida J, Siciliano S. 2001. Taxonomic diversity of bacteria associated with the roots of modern, recent and ancient wheat cultivars. *Biology and Fertility of Soils* **33(5)**:410–415 DOI 10.1007/s003740100343.

Giraudoux P, Antonietti JP, Beale C, Pleydell D, Treglia M. 2018. Package 'Pgirmess'. *Available at http://202901584/pub/pub/r/web/packages/pgirmess/pgirmess.pdf* (accessed on 01, February 2019).

Grayston SJ, ShenQuiang W, Campbell CD, Edwards AC. 1998. Selective influence of plant species on microbial diversity in the rhizosphere. *Soil Biology and Biochemistry* **30(3)**:369–378 DOI 10.1016/S0038-0717(97)00124-7.

Griffiths BS, Philippot L. 2013. Insights into the resistance and resilience of the soil microbial community. *FEMS Microbiology Reviews* **37(2)**:112–129 DOI 10.1111/j.1574-6976.2012.00343.x.

Guo J, McCulley RL, McNear DH. 2015. Tall fescue cultivar and fungal endophyte combinations influence plant growth and root exudate composition. *Frontiers in Plant Science* **6**:Article 183.

Gupta P, Sangwan N, Lal R, Vakhlu J. 2015. Bacterial diversity of drass, cold desert in Western Himalaya, and its comparison with antarctic and arctic. *Archives of Microbiology* **197(6)**:851–860 DOI 10.1007/s00203-015-1121-4.

Hancock DW, Curt Lacy R, Lawton Stewart R, Scott Tubbs R, Kichler J, Green TW, Hicks R. 2010. The management and use of bahiagrass. *Available at https://secure.caes.uga.edu/extension/publications/files/pdf/B%201362_4.PDF* (accessed on 01, February 2019).

Harrier LA, Watson CA. 2004. The potential role of Arbuscular Mycorrhizal (AM) fungi in the bioprotection of plants against soil-borne pathogens in organic and/or other sustainable farming systems. *Pest Management Science* **60(2)**:149–157 DOI 10.1002/ps.820.

Hawkes CV, Wren IF, Herman DJ, Firestone MK. 2005. Plant invasion alters nitrogen cycling by modifying the soil nitrifying community. *Ecology Letters* **8(9)**:976–985 DOI 10.1111/j.1461-0248.2005.00802.x.

Hayat R, Ali S, Amara U, Khalid R, Ahmed I. 2010. Soil beneficial bacteria and their role in plant growth promotion: a review. *Annals of Microbiology* **4(60)**:579–598.

Hiiesalu I, Pärtel M, Davison J, Gerhold P, Metsis M, Moora M, Öpik M, Vasar M, Zobel M, Wilson SD. 2014. Species richness of arbuscular mycorrhizal fungi: associations with grassland plant richness and biomass. *New Phytologist* **203(1)**:233–244 DOI 10.1111/nph.12765.

Hirata M. 2000. Effects of nitrogen fertiliser rate and cutting height on leaf appearance and extension in bahia grass (Paspalum Notatum) swards. *Tropical Grasslands* **34(1)**:7–13.

Ishikawa T, Subbarao GV, Ito O, Okada K. 2003. Suppression of nitrification and nitrous oxide emission by the tropical grass brachiaria humidicola. In: Abe J, ed. *Roots: the dynamic interface between plants and the earth: the 6th symposium of the international society of root research, 11–15 November 2001, Nagoya, Japan, Developments in Plant and Soil Sciences*. Dordrecht: Springer Netherlands, 413–419.

Jie W, Liu X, Cai B. 2013. Diversity of rhizosphere soil arbuscular mycorrhizal fungi in various soybean cultivars under different continuous cropping regimes. *PLOS ONE* **8(8)**:e72898 DOI 10.1371/journal.pone.0072898.

Johnson JM, Ludwig A, Furch A, Mithöfer A, Scholz SS, Reichelt M, Oelmüller R. 2019. The beneficial root-colonizing fungus mortierella hyalina promotes the aerial growth of arabidopsis and activates calcium-dependent responses which restrict alternaria brassicae-induced disease development in roots. *Molecular Plant-Microbe Interactions* **32(3)**:351–363.

Johnson AW, Minton NA, Brenneman TB, Burton GW, Culbreath AK, Gascho GJ, Baker SH. 1999. Bahiagrass, corn, cotton rotations, and pesticides for managing nematodes, diseases, and insects on peanut. *Journal of Nematology* **31(2)**:191–200.

Jones FP, Clark IM, King R, Shaw LJ, Woodward MJ, Hirsch PR. 2016. Novel european free-living, non-diazotrophic bradyrhizobium isolates from contrasting soils that lack nodulation and nitrogen fixation genes—a genome comparison. *Scientific Reports* **6**:25858 DOI 10.1038/srep25858.

Kaiser K, Wemheuer B, Korolkow V, Wemheuer F, Nacke H, Schöning I, Schrumpf M, Daniel R. 2016. Driving forces of soil bacterial community structure, diversity, and function in temperate grasslands and forests. *Scientific Reports* **6**:33696 DOI 10.1038/srep33696.

Kaneko T, Nakamura Y, Sato S, Minamisawa K, Uchiumi T, Sasamoto S, Watanabe A, Idesawa K, Iriguchi M, Kawashima K, Kohara M, Matsumoto M, Shimpo S, Tsuruoka H, Wada T, Yamada M, Tabata S. 2002. Complete genomic sequence of nitrogen-fixing symbiotic bacterium bradyrhizobium Japonicum USDA110. *DNA Research* **9**(**6**):189–197 DOI 10.1093/dnares/9.6.189.

Khan SA, Hamayun M, Yoon H, Kim H-Y, Suh S-J, Hwang S-K, Kim J-M, Lee I-J, Choo Y-S, Yoon U-H, Kong W-S, Lee B-M, Kim J-G. 2008. Plant growth promotion and penicillium citrinum. *BMC Microbiology* **8**(**1**):231 DOI 10.1186/1471-2180-8-231.

Khidir HH, Eudy DM, Porras-Alfaro A, Herrera J, Natvig DO, Sinsabaugh RL. 2010. A general suite of fungal endophytes dominate the roots of two dominant grasses in a semiarid grassland. *Journal of Arid Environments* **74**:35–42 DOI 10.1016/j.jaridenv.2009.07.014.

King DP, Chen C-I, Blanchard MT, Aldridge BM, Anderson M, Walker R, Maas J, Hanks D, Hall M, Stott JL. 2005. Molecular identification of a novel deltaproteobacterium as the etiologic agent of epizootic bovine abortion (foothill abortion). *Journal of Clinical Microbiology* **43**(**2**):604–609 DOI 10.1128/JCM.43.2.604-609.2005.

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AF, Bahram M, Bates ST, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan T, Eberhardt U, Dueñas M, Grebenc T, Griffith GW, Hartmann M, Kirk PM, Kohout P, Larsson E, Lindahl BD, Lücking R, Martín MP, Matheny PB, Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Põldmaa K, Saag L, Saar I, Schüßler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL, Telleria MT, Weiss M, Larsson KH. 2013. Towards a unified paradigm for sequence-based identification of fungi. *Molecular Ecology* **22**(**21**):5271–5277 DOI 10.1111/mec.12481.

Kourtev PS, Ehrenfeld JG, Häggblom M. 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology and Biochemistry* **7**(**35**):895–905.

Kowalchuk GA, Buma DS, De Boer W, Klinkhamer PGL, Van Veen JA. 2002. Effects of above-ground plant species composition and diversity on the diversity of soil-borne microorganisms. *Antonie Van Leeuwenhoek* **81**(**1–4**):509–520 DOI 10.1023/A:1020565523615.

Krishna KR, Bagyaraj DJ. 1984. Growth and nutrient uptake of peanut inoculated with the mycorrhizal fungus glomus fasciculatum compared with non-inoculated ones. *Plant and Soil* **77**(**2**):405–408 DOI 10.1007/BF02182946.

Kucey RMN. 1987. Increased phosphorus uptake by wheat and field beans inoculated with a phosphorus-solubilizing penicillium bilaji strain and with vesicular-arbuscular mycorrhizal fungi. *Applied and Environmental Microbiology* **53**(**12**):2699–2703.

Kundim BA, Itou Y, Sakagami Y, Fudou R, Iizuka T, Yamanaka S, Ojika M. 2003. New haliangicin isomers, potent antifungal metabolites produced by a marine myxobacterium. *The Journal of Antibiotics* **56**(**7**):630–638 DOI 10.7164/antibiotics.56.630.

Lange M, Eisenhauer N, Sierra CA, Bessler H, Engels C, Griffiths RI, Mellado-Vázquez PG, Malik AA, Roy J, Scheu S, Steinbeiss S, Thomson BC, Trumbore SE, Gleixner G. 2015. Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications* **6**:Article 6707 DOI 10.1038/ncomms7707.

Lata JC, Degrange V, Raynaud X, Maron PA, Lensi R, Abbadie L. 2004. Grass populations control nitrification in savanna soils. *Functional Ecology* **18**(**4**):605–611 DOI 10.1111/j.0269-8463.2004.00880.x.

Li H, Smith SE, Holloway RE, Zhu Y, Andrew Smith F. 2006. Arbuscular mycorrhizal fungi contribute to phosphorus uptake by wheat grown in a phosphorus-fixing soil even in the absence of positive growth responses. *The New Phytologist* **172**(**3**):536–543 DOI 10.1111/j.1469-8137.2006.01846.x.

Li J, Zou C, Xu J, Ji X, Niu X, Yang J, Huang X, Zhang K-Q. 2015. Molecular mechanisms of nematode-nematophagous microbe interactions: basis for biological control of plant-parasitic nematodes. *Annual Review of Phytopathology* **53**:67–95 DOI 10.1146/annurev-phyto-080614-120336.

Liu H, Hull RJ, Duff DT. 1997. Comparing cultivars of three cool-season turfgrasses for soil water NO3- concentration and leaching potential. *Crop Science* **37**(**2**):526–534 DOI 10.2135/cropsci1997.0011183X003700020036x.

Lugtenberg B, Kamilova F. 2009. Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology* **63**:541–556 DOI 10.1146/annurev.micro.62.081307.162918.

Lundberg DS, Yourstone S, Mieczkowski P, Jones CD, Dangl JL. 2013. Practical innovations for high-throughput amplicon sequencing. *Nature Methods* **10**(**10**):999–1002 DOI 10.1038/nmeth.2634.

Maherali H, Klironomos JN. 2007. Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* **316**(**5832**):1746–1748 DOI 10.1126/science.1143082.

Martin M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.Journal* **17**(**1**):10–12.

McCaig AE, Glover LA, Prosser JI. 1999. Molecular analysis of bacterial community structure and diversity in unimproved and improved upland grass pastures. *Applied and Environmental Microbiology* **65**(**4**):1721–1730.

Mesa S, Göttfert M, Bedmar EJ. 2001. The nir, nor, and nos denitrification genes are dispersed over the bradyrhizobium japonicum chromosome. *Archives of Microbiology* **176**(**1**):136–142 DOI 10.1007/s002030100305.

Miki T, Ushio M, Fukui S, Kondoh M. 2010. Functional diversity of microbial decomposers facilitates plant coexistence in a plant–microbe–soil feedback model. *Proceedings of the National Academy of Sciences of the United States of America* **107**(**32**):14251–14256 DOI 10.1073/pnas.0914281107.

Miller HJ, Henken G, Veen JAV. 1989. Variation and composition of bacterial populations in the rhizospheres of maize, wheat, and grass cultivars. *Canadian Journal of Microbiology* **35**(**6**):656–660.

Nacke H, Thürmer A, Wollherr A, Will C, Hodac L, Herold N, Schöning I, Schrumpf M, Daniel R. 2011. Pyrosequencing-based assessment of bacterial community

structure along different management types in german forest and grassland soils. *PLOS ONE* **6(2)**:e17000 DOI 10.1371/journal.pone.0017000.

National Cooperative Soil Survey U.S.A.. 2019. Official series description—orangeburg series. *Available at https://soilseries.sc.egov.usda.gov/osd_docs/o/orangeburg.html* (accessed on 01 February 2019).

Newman Y, Vendramini J, Blount A. 2011. Bahiagrass (Paspalum Notatum): overview and management. *Available at http://edis.ifas.ufl.edu/ag342* (accessed on 01 February 2019).

Nguyen NH, Smith D, Peay K, Kennedy P. 2015. Parsing ecological signal from noise in next generation amplicon sequencing. *The New Phytologist* **205(4)**:1389–1393 DOI 10.1111/nph.12923.

Nunoura T, Takaki Y, Hirai M, Shimamura S, Makabe A, Koide O, Kikuchi T, Miyazaki J, Koba K, Yoshida N, Sunamura M, Takai K. 2015. Hadal biosphere: insight into the microbial ecosystem in the deepest ocean on earth. *Proceedings of the National Academy of Sciences of the United States of America* **112(11)**:E1230–E1236 DOI 10.1073/pnas.1421816112.

Oehl F, Sieverding E, Ineichen K, Ris EA, Boller T, Wiemken A. 2005. Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. *New Phytologist* **165(1)**:273–283.

Oksanen J. 2017. Vegan: ecological diversity. *Available at https://cran.r-project.org/web/packages/vegan/vegan.pdf* (accessed on 01 February 2019).

Oliveira JA, West CP, Afif E, Palencia P. 2017. Comparison of miscanthus and switchgrass cultivars for biomass yield, soil nutrients, and nutrient removal in northwest spain. *Agronomy Journal* **109(1)**:122–130 DOI 10.2134/agronj2016.07.0440.

Oniki M, Kobayashi K, Araki T, Ogoshi A. 1986. A new disease of turf-grass caused by binucleate Rhizoctonia AG-Q. *Japanese Journal of Phytopathology* **52(5)**:850–853 DOI 10.3186/jjphytopath.52.850.

Orgiazzi A, Lumini E, Henrik Nilsson R, Girlanda M, Vizzini A, Bonfante P, Bianciotto V. 2012. Unravelling soil fungal communities from different mediterranean land-use backgrounds. *PLOS ONE* **7(4)**:e34847 DOI 10.1371/journal.pone.0034847.

Osorio NW, Habte M. 2001. Synergistic influence of an arbuscular mycorrhizal fungus and a P solubilizing fungus on growth and p uptake of leucaena leucocephala in an oxisol. *Arid Land Research and Management* **15(3)**:263–274 DOI 10.1080/15324980152119810.

Osorio NW, Habte M. 2013. Synergistic effect of a phosphate-solubilizing fungus and an arbuscular mycorrhizal fungus on leucaena seedlings in an oxisol fertilized with rock phosphate. *Botany* **91(4)**:274–281 DOI 10.1139/cjb-2012-0226.

Osorio NW, Habte M. 2014. Soil phosphate desorption induced by a phosphate-solubilizing fungus. *Communications in Soil Science and Plant Analysis* **45(4)**:451–460 DOI 10.1080/00103624.2013.870190.

O'Sullivan CA, Fillery IRP, Roper MM, Richards RA. 2016. Identification of several wheat landraces with biological nitrification inhibition capacity. *Plant and Soil* **404(1)**:61–74 DOI 10.1007/s11104-016-2822-4.

Pfister DH. 1997. Castor, pollux and life histories of fungi. *Mycologia* **89(1)**:1–23 DOI 10.1080/00275514.1997.12026750.

Porras-Alfaro A, Bayman P. 2011. Hidden fungi, emergent properties: endophytes and microbiomes. *Annual Review of Phytopathology* **49**:291–315 DOI 10.1146/annurev-phyto-080508-081831.

Quast C, Pruesse E, Yilmaz P, Gerken J, Schweer T, Yarza P, Peplies J, Oliver Glöckner F. 2013. The SILVA Ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Research* **41(D1)**:D590–D596.

R Core Team. 2017. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. *Available at https://www.r-project.org*.

Reichenbach H, Höfle G. 1993. Biologically active secondary metabolites from myxobacteria. *Biotechnology Advances* **11(2)**:219–277 DOI 10.1016/0734-9750(93)90042-L.

Reynolds HL, Packer A, Bever JD, Clay K. 2003. Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology* **84(9)**:2281–2291 DOI 10.1890/02-0298.

Rodrigues RR, Moon J, Zhao B, Williams MA. 2016. Microbial communities and diazotrophic activity differ in the root-zone of alamo and dacotah switchgrass feedstocks. *GCB Bioenergy* **9(6)**:1057–1070.

Rodriguez-Kabana R, Weaver DB, Garcia R, Robertson DG, Carden EL. 1989. Bahiagrass for the management of root-knot and cyst nematodes in soybean. *Nematropica* **19(2)**:185–193.

Rodriguez-Kabana R, Weaver CF, Robertson DG, Ivey H. 1988. Bahiagrass for the Management of Meloidogyne Arenaria in Peanut. *Journal of Nematology* **20(2)**:110–114.

Rognes T, Flouri T, Nichols B, Quince C, Mahé F. 2016. VSEARCH: a versatile open source tool for metagenomics. *PeerJ* **4**:e2584 DOI 10.7717/peerj.2584.

Rubner A. 1996. Revision of predacious hyphomycetes in the dactylella-monacrosporium complex. *Studies in Mycology* **39**:1–134.

Ruiz-Lozano JM, Azcon R, Gomez M. 1995. Effects of arbuscular-mycorrhizal glomus species on drought tolerance: physiological and nutritional plant responses. *Applied and Environmental Microbiology* **61(2)**:456–460.

Schwarzott D, Walker C, Schüssler A. 2001. Glomus, the largest genus of the arbuscular mycorrhizal fungi (glomales), is nonmonophyletic. *Molecular Phylogenetics and Evolution* **21(2)**:190–197 DOI 10.1006/mpev.2001.1007.

Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Lonsdorf EV, Whitham TG, Hart SC. 2008. Plant-soil-microorganism interactions: heritable relationship between plant genotype and associated soil microorganisms. *Ecology* **89(3)**:773–781 DOI 10.1890/07-0337.1.

Scott JM. 1920. Bahia grass. *Agronomy Journal* **12(3)**:112–113 DOI 10.2134/agronj1920.00021962001200030004x.

Selosse M, Baudoin E, Vandenkoornhuyse P. 2004. Symbiotic microorganisms, a key for ecological success and protection of plants. *Comptes Rendus Biologies* **327(7)**:639–648 DOI 10.1016/j.crvi.2003.12.008.

Shade A, Peter H, Allison SD, Baho D, Berga M, Buergmann H, Huber DH, Langenheder S, Lennon JT, Martiny JBH, Matulich KL, Schmidt TM, Handelsman J.

2012. Fundamentals of microbial community resistance and resilience. *Frontiers in Microbiology* **3**.

Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA. 2013. Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. *SpringerPlus* **2**:Article 587 DOI 10.1186/2193-1801-2-587.

Sharp KH, Eam B, Faulkner DJ, Haygood MG. 2007. Vertical transmission of diverse microbes in the tropical sponge corticium sp. *Applied and Environmental Microbiology* **73(2)**:622–629 DOI 10.1128/AEM.01493-06.

Singh RJ. 2009. Genetic resources, chromosome engineering, and crop improvement: forage crops. *CRC Press* **5**:1–320.

Smith SE, Smith FA, Jakobsen I. 2003. Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. *Plant Physiology* **133(1)**:16–20 DOI 10.1104/pp.103.024380.

Smith SE, Mette Grønlund IJ, Andrew Smith F. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiology* **156(3)**:1050–1057 DOI 10.1104/pp.111.174581.

Smith S, Read D. 2008. *Mycorrhizal symbiosis*. London: Academic Press.

Somers E, Vanderleyden J, Srinivasan M. 2004. Rhizosphere bacterial signalling: a love parade beneath our feet. *Critical Reviews in Microbiology* **30(4)**:205–240 DOI 10.1080/10408410490468786.

Subbarao GV, Ishikawa T, Ito O, Nakahara K, Wang HY, Berry WL. 2006. A bioluminescence assay to detect nitrification inhibitors released from plant roots: a case study with brachiaria humidicola. *Plant and Soil* **288(1)**:101–112 DOI 10.1007/s11104-006-9094-3.

Subbarao GV, Nakahara K, Hurtado MP, Ono H, Moreta DE, Salcedo AF, Yoshihashi AT, Ishikawa T, Ishitani M, Ohnishi-Kameyama M, Yoshida M, Rondon M, Rao IM, Lascano CE, Berry WL, Ito O. 2009. Evidence for biological nitrification inhibition in brachiaria pastures. *Proceedings of the National Academy of Sciences of the United States of America* **106(41)**:17302–17307 DOI 10.1073/pnas.0903694106.

Summerell BA, Laurence MH, Liew ECY, Leslie JF. 2010. Biogeography and phylogeography of fusarium: a review. *Fungal Diversity* **44(1)**:3–13 DOI 10.1007/s13225-010-0060-2.

Sumner DR, Minton NA, Brenneman TB, Burton GW, Johnson AW. 1999. Root diseases and nematodes in bahiagrass-vegetable rotations. *Plant Disease* **83(1)**:55–59 DOI 10.1094/PDIS.1999.83.1.55.

Sun L, Lu Y, Yu F, Kronzucker HJ, Shi W. 2016. Biological nitrification inhibition by rice root exudates and its relationship with nitrogen-use efficiency. *New Phytologist* **212(3)**:646–656 DOI 10.1111/nph.14057.

Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Villarreal Ruiz L, Vasco-Palacios AM, Quang Thu P, Suija A, Smith ME, Sharp C, Saluveer E, Saitta A, Rosas M, Riit T, Ratkowsky D, Pritsch K, Põldmaa K, Piepenbring

M, Phosri C, Peterson M, Parts K, Pärtel K, Otsing E, Nouhra E, Njouonkou AL, Henrik Nilsson R, Morgado LN, Mayor J, May TW, Majuakim L, Jean Lodge D, See Lee S, Larsson K-H, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo L-D, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, Dang T, Chen X, Buegger F, Brearley FQ, Bonito G, Anslan S, Abell S, Abarenkov K. 2014. Global diversity and geography of soil fungi. *Science* **346(6213)**:Article 125668 DOI 10.1126/science.1256688.

Thomson BC, Ostle N, McNamara N, Bailey MJ, Whiteley AS, Griffiths RI. 2010. Vegetation affects the relative abundances of dominant soil bacterial taxa and soil respiration rates in an upland grassland soil. *Microbial Ecology* **59(2)**:335–343 DOI 10.1007/s00248-009-9575-z.

Trenholm LE, Cisar JL, Unruh JB. 2011. Bahiagrass for florida lawns. ENH 6 University of Florida, Institute of Food and Agricultural Sciences, Gainesville, USA. *Available at http://edis.ifas.ufl.edu/pdffiles/LH/LH00600.pdf* (accessed on 09, February 2019).

Uehling J, Gryganskyi A, Hameed K, Tschaplinski T, Misztal PK, Wu S, Desirò A, Vande Pol N, Du Z, Zienkiewicz A, Zienkiewicz K, Morin E, Tisserant E, Splivallo R, Hainaut M, Henrissat B, Ohm R, Kuo A, Yan J, Lipzen A, Nolan M, LaButti K, Barry K, Goldstein AH, Labbé J, Schadt C, Tuskan G, Grigoriev I, Martin F, Vilgalys R, Bonito G. 2017. Comparative genomics of mortierella elongata and its bacterial endosymbiont mycoavidus cysteinexigens. *Environmental Microbiology* **19(8)**:2964–2983 DOI 10.1111/1462-2920.13669.

Van Loon LC, Bakker PAHM, Pieterse CMJ. 1998. Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology* **36**:453–483 DOI 10.1146/annurev.phyto.36.1.453.

Vandenkoornhuyse P, Ridgway KP, Watson IJ, Fitter AH, Young JPW. 2003. Co-existing grass species have distinctive arbuscular mycorrhizal communities. *Molecular Ecology* **12(11)**:3085–3095 DOI 10.1046/j.1365-294X.2003.01967.x.

Van der Heijden MGA, Bardgett RD, Van Straalen NM. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* **11(3)**:296–310 DOI 10.1111/j.1461-0248.2007.01139.x.

Van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396(6706)**:69–72 DOI 10.1038/23932.

Vessey JK. 2003. Plant growth promoting rhizobacteria as biofertilizers. *Plant and Soil* **255(2)**:571–586 DOI 10.1023/A:1026037216893.

Vurukonda SSKP, Vardharajula S, Shrivastava M, SkZ A. 2016. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiological Research* **184**:13–24 DOI 10.1016/j.micres.2015.12.003.

Wagner L, Stielow B, Hoffmann K, Petkovits T, Papp T, Vágvölgyi C, De Hoog GS, Verkley G, Voigt K. 2013. A comprehensive molecular phylogeny of the mortierellales (mortierellomycotina) based on nuclear ribosomal DNA. *Persoonia: Molecular Phylogeny and Evolution of Fungi* **30**:77–93 DOI 10.3767/003158513X666268.

Wakelin SA, Warren RA, Harvey PR, Ryder MH. 2004. Phosphate solubilization by penicillium spp. closely associated with wheat roots. *Biology and Fertility of Soils* **40**(**1**):36–43 DOI 10.1007/s00374-004-0750-6.

Wang F, Liu R, Lin X, Zhou J. 2003. Comparison of diversity of arbuscular mycorrhizal fungi in different ecological environments. *Acta Ecologica Sinica* **23**(**12**):2666–2671.

Warcup JH. 1951. Ecology of soil fungi. *Transactions of the British Mycological Society* **34**(**3**):376–399 DOI 10.1016/S0007-1536(51)80065-2.

Ward NL, Challacombe JF, Janssen PH, Henrissat B, Coutinho PM, Wu M, Xie G, Haft DH, Sait M, Badger J, Barabote RD, Bradley B, Brettin TS, Brinkac LM, Todd Creasy DB, Daugherty SC, Davidsen TM, DeBoy RT, Chris Detter J, Dodson RJ, Scott Durkin A, Ganapathy A, Gwinn-Giglio M, Han CS, Khouri H, Kiss H, Kothari SP, Madupu R, Nelson KE, Nelson WC, Paulsen I, Penn K, Ren Q, Rosovitz MJ, Selengut JD, Shrivastava S, Sullivan SA, Tapia R, Sue Thompson L, Watkins KL, Yang Q, Yu C, Zafar N, Zhou L, Kuske CR. 2009. Three genomes from the phylum acidobacteria provide insight into the lifestyles of these microorganisms in soils. *Applied and Environmental Microbiology* **75**(**7**):2046–2056 DOI 10.1128/AEM.02294-08.

Wardle DA, Bardgett RD, Klironomos JN, Setala H, Van der Putten WH, Wall DH. 2004. Ecological linkages between aboveground and belowground biota. *Science* **304**(**5677**):1629–1633 DOI 10.1126/science.1094875.

Wedin DA, Tilman D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* **84**(**4**):433–441 DOI 10.1007/BF00328157.

Wehner J, Antunes PM, Powell JR, Mazukatow J, Rillig MC. 2010. Plant pathogen protection by arbuscular mycorrhizas: a role for fungal diversity? *Pedobiologia—Journal of Soil Ecology* **3**(**53**):197–201.

Weller DM, Raaijmakers JM, McSpadden Gardener BB, Thomashow LS. 2002. Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annual Review of Phytopathology* **40**:309–348 DOI 10.1146/annurev.phyto.40.030402.110010.

Wenzel SC, Müller R. 2009. Myxobacteria—'microbial factories' for the production of bioactive secondary metabolites. *Molecular BioSystems* **5**(**6**):567–574 DOI 10.1039/b901287g.

Whitelaw MA, Harden TJ, Bender GL. 1997. Plant growth promotion of wheat inoculated with penicillium radicumsp. nov. *Soil Research* **35**(**2**):291–300 DOI 10.1071/S96040.

Wiesler F, Horst WJ. 1993. Differences among maize cultivars in the utilization of soil nitrate and the related losses of nitrate through leaching. *Plant and Soil* **151**(**2**):193–203 DOI 10.1007/BF00016284.

Will C, Thürmer A, Wollherr A, Nacke H, Herold N, Schrumpf M, Gutknecht J, Wubet T, Buscot F, Daniel R. 2010. Horizon-specific bacterial community composition of german grassland soils, as revealed by pyrosequencing-based analysis of 16S RRNA genes. *Applied and Environmental Microbiology* **76**(**20**):6751–6759 DOI 10.1128/AEM.01063-10.

Wilson GPM. 1987. Paspalum notatum flügge (bahia grass) cv. competidor (Reg. No. A-7c-1). *Tropical Grasslands* **21**:93–94.

Wu QS, Zou YN, Xia RX. 2006. Effects of water stress and arbuscular mycorrhizal fungi on reactive oxygen metabolism and antioxidant production by citrus (citrus tangerine) roots. *European Journal of Soil Biology* **3(42)**:166–172.

Xu M, Li X, Cai X, Li X, Christie P, Zhang J. 2017. Land use alters arbuscular mycorrhizal fungal communities and their potential role in carbon sequestration on the tibetan plateau. *Scientific Reports* **7(1)**:Article 3067.

Yang Y, Dou Y, Huang Y, An S. 2017. Links between soil fungal diversity and plant and soil properties on the loess plateau. *Frontiers in Microbiology* **8**:Article 2198.

Yang J, Kloepper JW, Ryu C-M. 2009. Rhizosphere bacteria help plants tolerate abiotic stress. *Trends in Plant Science* **14(1)**:1–4 DOI 10.1016/j.tplants.2008.10.004.

Zahran HH. 1999. Rhizobium-legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiology and Molecular Biology Reviews* **63(4)**:968–989.

Zak DR, Holmes W, White DC, Peacock AD, Tilman D. 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology* **84(8)**:2042–2050 DOI 10.1890/02-0433.

Zakir HAKM, Subbarao GV, Pearse SJ, Gopalakrishnan S, Ito O, Ishikawa T, Kawano N, Nakahara K, Yoshihashi T, Ono H, Yoshida M. 2008. Detection, isolation and characterization of a root-exuded compound, methyl 3-(4-hydroxyphenyl) propionate, responsible for biological nitrification inhibition by sorghum (sorghum bicolor). *The New Phytologist* **180(2)**:442–451 DOI 10.1111/j.1469-8137.2008.02576.x.

Zhang H, Wu X, Li G, Qin P. 2011. Interactions between arbuscular mycorrhizal fungi and phosphate-solubilizing fungus (mortierella sp.) and their effects on kostelelzkya virginica growth and enzyme activities of rhizosphere and bulk soils at different salinities. *Biology and Fertility of Soils* **5(47)**:543–554.

Zhou J, Xia B, Huang H, Treves DS, Hauser LJ, Mural RJ, Palumbo AV, Tiedje JM. 2003. Bacterial phylogenetic diversity and a novel candidate division of two humid region, sandy surface soils. *Soil Biology and Biochemistry* **7(35)**:915–924.