Influence of Tall Fescue *Epichloë* endophytes on Rhizosphere Soil Microbiome

Kishan Mahmud
University of Georgia College of Agricultural and Environmental Sciences https://orcid.org/0000-0001-5479-1475

Kendall Lee
University of Georgia College of Agricultural and Environmental Sciences

Nicholas Hill
University of Georgia College of Agricultural and Environmental Sciences

Ali Missaoui (cssamm@uga.edu)
University of Georgia https://orcid.org/0000-0003-1710-1142

Research

Keywords: Tall fescue, soil microbiome, fungal endophyte, plant-soil interaction, functional redundancy

Posted Date: June 22nd, 2021

DOI: https://doi.org/10.21203/rs.3.rs-614409/v1

Abstract

Background Tall fescue (*Lolium arundinaceum* (Schreb.) S.J. Darbyshire) is a popular perennial grass species for livestock production and amenities in the United States. Tall fescue often forms a symbiotic relationship with fungal endophytes (*Epichloë coenophiala*) which provides increased plant tolerance to environmental stress compared to endophyte-free plants. However, whether this improved plant performance is the sole result of the unique relationship between the grass and the shoot-dwelling fungal endophyte of rhizosphere origin remains a question. This symbiosis possibly regulates the recruitment of beneficial soil microbial communities in endophyte-infected tall fescue rhizosphere and may offer enhanced nutrients and water acquisition, thereby, providing the plant with an increased tolerance level against environmental stresses. We compared the soil bacterial and fungal community composition and investigated possible community shifts in soil microbial populations based on endophyte infection in tall fescue by analyzing the 16s rRNA gene and ITS specific region.

Results Our data revealed that bacterial community richness and the evenness indicated by Shannon Diversity Index (SDI) was greater than 4 in both endophyte-infected and endophyte-free tall fescue soil. In both types tall fescue soil, the prominent bacterial families were Planctomycetaceae, Balstocatellaceae_(subgroup_4), Chitinophagaceae, and Bacillaceae. In the case of soil fungal diversity, the SDI was overall low and ranged between 1.21 for endophyte-free and 1.27 for endophyte-infected tall fescue soil. The prominent fungal phyla were Basidiomycota and Ascomycota, and we observed a clear fungal community difference between endophyte-infected and endophyte-free soil at the phylum level. Moreover, endophyte-infected tall fescue soil showed a greater diversity at the genus level compared to endophyte-free tall fescue soil. In addition, plant-available soil phosphorus (P) is also influenced by the presence of endophytes in tall fescue.

Conclusion Our results indicate that there is a tripartite relationship between tall fescue, the presence of fungal endophyte in the tall fescue, and the below-ground soil fungal communities. The dynamic of this three-way interaction perhaps contributes to the nutrient acquisition and stress tolerance by tall fescue possibly by recruiting a diverse array of potentially beneficial soil microbes.

Background

Grasses cover almost 20% of the total land area on the planet [1] and are widely distributed ecosystems [2]. They offer important ecosystem services such as providing forage for livestock [3], soil carbon sequestration [4], improved runoff quality [5], erosion control, climate regulation [6], and resistance to invasive species [7]. Many grass species are known to form symbiotic relationships with fungal endophytes [8] that led to eventual plant colonization of terrestrial environments [9]. Tall fescue (*Lolium arundinaceum* (Schreb.) S.J. Darbyshire), a cool-season perennial grass [10] is cultivated on an estimated 14 million hectares in the United States [11]. Tall fescue often forms a interdependent relationship with a shoot-specific endophyte (*Epichloë coenophiala*) of fungal origin that produces ergot alkaloids toxic to livestock, causing *fescue toxicosis* or *fescue foot* [12, 13]. To avoid *fescue toxicosis*, novel endophytes

were identified and introduced into different tall fescue cultivars with non-toxic alkaloids such as lolines and peramines [14]. Although detrimental to livestock, tall fescue infected with *Epichloë coenophiala* has shown to be persistent, exhibit better plant fitness, and offer improved ecosystem services over other grass species in pastures [15, 16]. Endophyte dwelling tall fescue plants is a unique model to investigate the potential relationships between above and belowground microbial communities. This potential relationship between the tall fescue, the endophyte, and the soil microbial communities might provide important insights to explore and clarify the plant's resilience against environmental stress and climate change, different soil biogeochemical processes that influence soil health, and vital ecosystem services. It is well documented that soil microbial communities impart significant benefits in soil nutrient cycling, soil fertility status, and soil carbon sequestration that influences plant fitness and survival in varying terrestrial ecosystems [17–19].

The soil microbiome composition is at the forefront of evolutionary ecology where the primordial focus is on the identification of the beneficial microbial communities and comprehend the extent of influence on plant performance and soil health [20, 21]. Soil nutrient status plays a central role in impacting soil bacterial and fungal communities. This is particularly true for phosphorus (P), the least mobile macronutrient, in the soil of the southeastern USA [22]. Due to its fixation with insoluble mineral-complex with iron (Fe) and aluminum (Al) oxides in acidic soil and with calcium (Ca) in alkaline soil, P is often limited to be released into the soil solution for root uptake [23, 24]. Thus, endophyte infection in tall fescue may offer a competitive advantage to non-infected fescue by influencing the soil microbial processes and soil microbial communities [25–27]. Additionally, the quantity and type of root exudates and rhizodeposits change with different stages of plant development [28–30], thus, creating a resource partitioning in the soil that subsequently leads to niche partitioning [31–33]. In turn, given the rhizosphere origin of endophytic microbial populations, soil bacterial and fungal community composition may regulate the plant endophytic diversity and community composition [34]. In earlier studies, based on the endophyte infection in tall fescue, shifts in soil microbial (bacterial and fungal) community structure, and soil food web has been reported [35, 36]. These plant-fungal associations, especially in grass species, define a significant two-faceted interaction; i) the collaboration gradient (above-ground) [37] and ii) root exudates mediated influence (below-ground) [38]. The first interaction describes how the plant-fungal symbiosis impacts nutrient foraging, promotes plant growth [39], provides resilience against abiotic stress such as drought and salt tolerance [40], and biotic stress such as plant pathogens [41]. The second interaction highlights the fungal communities associated with the rhizosphere communities, facilitates soil nutrient cycling and nutrient acquisition [42], organic matter decomposition [43, 44], synthesis of phytohormones for root utilization [45], resistance against nematodes [46], and protection against pathogens [47]. Thus, determining the endophyte-facilitated soil microbial processes and the subsequent soil microbial response contributing to increased plant production and stress tolerance may carry significant economic and ecological importance for sustainable agricultural practices [48]. Our objective was to explore the diversity of the soil bacterial and fungal communities associated with tall fescue rhizosphere and investigate whether the bacterial and fungal population differ based on the presence of endophyte in tall fescue.

Methods

Site description

The study site was in the southeastern USA at the J. Phil Campbell (JPC) Research and Education Center (33° 52' N, 83° 27'W) and Iron Horse Farm (IHF) (33° 72' N, 83° 30'W) in Watkinsville, Georgia. The soil at JPC is a fine kaolinitic, thermic Typic Kanhapludults in the Cecil sandy loam series with a 2 to 6% slope and the soil at IHF is Pacolet sandy clay loam, with a 6 to 10 percent slope [49]. The region has 123 cm average annual rainfall and an average minimum and maximum temperature of 10.4°C and 22.5°C, respectively. Since its establishment in the fall of 2014, the tall fescue plants experienced two summers of unusually higher temperatures in summer 2016 and summer 2019 (Table 1). Soil sampling for this study was done in October 2019, following a summer that according to the National Oceanic and Atmospheric Administration had the hottest July on record, since the late 1800s.

Table 1

Average maximum, minimum, and daily atmospheric temperature (^{0}C), average soil temperature (0–15 cm) (^{0}C), and average rainfall (mm) during summer months (June, July, and August) from 2015 to 2019.

Season	Maximum Atmospheric Temperature (^{0}C)	Minimum Atmospheric Temperature (^{0}C)	Daily Atmospheric Temperature (^{0}C)	Daily Soil Temperature (^{0}C) at 15 cm depth	Average Rainfall (mm)
Summer 2015	32	21	26	28	391
Summer 2016	33	21	27	30	295
Summer 2017	30	20	25	28	517
Summer 2018	31	20	25	28	392
Summer 2019	31	20	25	29	304

Soil Sampling and Tall Fescue Plants

We sampled soil from 48 different tall fescue accessions rhizosphere with a hand soil probe (2.5-cm diameter) to a depth of 0–15 cm. All soil samples were kept refrigerated at 4°C. The soils were then were air-dried, ground, and passed through a 2-mm sieve for soil nutrient analysis. For microbial analysis, soil samples were immediately separated and kept at − 20°C until the soil genomic DNA was extracted (DNA extraction and sequencing). Out of 48 tall fescue ranges, 43 ranges were planted at JPC and five were at the IHF site. We selected nine tall fescue cultivars with no endophytes (E-), 35 cultivars with endophyte

infection (E+), among which 21 were infected with novel-endophytes and 14 were wild-type, toxic endophytes.

DNA Extraction, PCR Amplification, and 16S rRNA Gene and ITS Gene Sequencing

From homogenized and frozen soil (0.25 g), soil DNA was extracted using DNA, QIAGEN DNeasy PowerSoil Kit (DNeasy PowerSoil Kit Handbook, May 2017, Qiagen, Valencia, CA, USA). Soil DNA quality and concentration was assessed by A NanoDrop 2000 spectrophotometer (Thermo Scientific, Waltham, Massachusetts, USA). Extracts were stored at − 20°C until further analyses. A bacterial sequencing library targeting the bacterial 16S rRNA genes was prepared using primers sets from PacBio 16S protocol (V1-V9 regions) [50]; 27F27F (AGRGTTYGATYMTGGCTCAG)/ 14292R (RGYTACCTTGTTACGACTT). For the fungal sequencing library, we targeted the ITS region and used ITS1-F Forward (CTTGGTCATTTAGAGGAAGTAA)/ ITS2-R Reverse (GCTGCGTTCTTCATCGATGC) to amplify the ITS region. The sequencing workflow was as flowed: Multiplexing with PacBio Barcoded Universal Primers > AMPure PB bead purification > Pooling Barcoded Amplicons > SMRTbell Library Construction > Purification of SMRTbell Templates > Anneal and Bind SMRTbell Templates > Sequencing on PacBio Sequel II System. The first-round amplification PCR conditions were 95°C for 180 sec, followed by 20 cycles of 95°C for 30 s, 57°C for 30 s, and 72°C for 60 s with universal primer-tailed 16S primers and ITS1 primers. The second-round amplification PCR conditions were 95°C for 30 s, 57°C for 30 s, and 72°C for 60 s for 20 cycles with PacBio Barcoded Universal Primers and SMRTbell libraries were prepared by using PacBio Barcoded Universal Primers for Multiplex SMRT Sequencing. Then PacBio's single-molecule circular consensus sequencing (CCS) reads were generated for full-length 16S rRNA genes and ITS gene (accuracy of 99%). The CCS reads were demultiplexed using the software "lima" in SMRT Analysis software version 2.3.0. to generate bam files followed by a conversion to Fastq files via bam2fastq.

Data Analysis

The CCS reads were processed with DADA2 software packages (16S rRNA gene and ITS specific workflow) (version 1.8) [51], and analyzed with phyloseq for alpha and beta diversity (version 1.25.2) [52]. For 16s rRNA gene CCS data, the DADA2 workflow follows primer trimming, quality filtering, and dereplication. Amplicon sequence variants (ASVs) were inferred after learning the error rates. Afterward, the "removeBimeraDenovo" command was used to remove chimeras. Finally, we used the the SILVA nr v132 train set to assign taxonomy. For the fungal data analysis, we followed the ITS-specific variation of the DADA2 package. In the fungal DADA2 workflow, after orienting the primers, we used a specialized primer/adapter removal tool "cutadapt" [53]. After primer removal, the steps are quality filtering, dereplication, inferring ASVs after error learning, and finally removing chimeras. We used UNITE ITS database for taxonomic assignments [54]. The ASV tables from DADA2 pipelines were imported into phyloseq to make phyloseq object and to calculate alpha and beta diversity.

Statistical Analysis

Analysis of variance with JMP PRO 15 software (JMP®, Version 15. SAS Institute Inc., Cary, NC, 1989–2019) was used to determine differences in soil pH, inorganic nitrogen, and nitrate content, calcium,

potassium, magnesium, phosphorus, and zinc between endophyte-free fescue soil, non-toxic endophyte-infected fescue soil and toxic endophyte-infected fescue soil samples ($p < 0.05$). Comparisons between multiple means of different soil nutrient content were done with Tukey's HSD ($p < 0.05$).

Results

Soil Chemical Properties

The research plots were established in the fall of 2014 with 750 different tall fescue accessions. Since its establishment, the plots were fertilized with inorganic fertilizers (N-P-K) in October 2014 and regular clippings of the grass were performed every spring. There were no significant differences in soil pH and soil nutrient content between E- and E + tall fescue soil, except for plant-available phosphorus in soil (Table 2). The E + tall fescue soil had higher plant-available P compared to the E- tall fescue soil. Between endophyte-free, non-toxic, and toxic endophyte-infected tall fescue soil, non-toxic endophyte-infected soil had significantly greater plant-available P compared to the rest (Table 2). Although, Zn content in soil was not statistically significant between the E- and E + tall fescue soil, three endophytes infected tall fescue soil samples, accession 1062, 1064, and Bar Optima had higher soil Zn content.

Table 2

Mean soil nitrogen (N), calcium (Ca), potassium (K), magnesium (Mg), manganese (Mn), phosphorus (P), and zinc (Zn) (mg/kg) content.

	pH	NH_4^+-N	NO_3^-N	Ca	K	Mg	Mn	P	Zn
Endophyte Free Soil	6.53^a	3 ^{a}	244 ^{a}	801^a	40^a	105^a	17^a	26^b	1.0^a
Endophyte Infected Soil (Toxic)	6.59^a	2 ^{a}	270 ^{a}	681^a	43^a	93^a	17^a	38^a	1.17^a
Endophyte Infected Soil (Non-toxic)	6.59^a	3 ^{a}	245 ^{a}	731^a	45^a	99^a	16^a	33^{ab}	1.07^a

Different lower-case letters indicate a significant difference between endophyte-free soil, toxic endophyte-infected soil, and non-toxic endophyte-infected soil ($p < 0.05$)

Soil Bacterial Abundance, Diversity, And Community Composition

We identified 1212 and 3411 bacterial amplicon sequence variants (ASVs) in the E- and E + tall fescue soil collected from the tall fescue plots, respectively. We identified 18 phyla, 29 classes, 72 orders, 111 families, and 151 bacterial genera in E + tall fescue soil. In E^- tall fescue soil we identified, 14 phyla, 29 classes, 45 orders, 88 families, and 97 bacterial genera. The Shannon diversity index (SDI) highlights the species richness and evenness of the species among the entire community; the higher number indicates higher diversity. Calculations of the SDI showed that bacterial communities in the E- tall fescue soil were

higher (mean H' = 4.5) compared to E + soil (mean H' = 4.0). However, this difference in Shannon Index was not statistically significant. Additionally, bacterial beta-diversity presented with principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarities showed no significant differences between soil microbial communities based on the presence of endophyte in tall fescue. The prominent bacterial phylum in both E- and E + tall fescue soil was Planctomycetes (Fig. 1a and 1b). In E + tall fescue soil, the abundance of phyla from greatest to lowest was as follows: Planctomycetes (28%) > Proteobacteria (20%) > Acidobacteria (12%) > Bacteroidetes (9%) > Firmicutes (6%) > Verrucomicrobia, Chloroflexi and Actinobacteria (5%) > Gemmatimonadetes and Nitrospira (2%) (Fig. 1a). For E- tall fescue soil, from greatest to lowest abundance of the prominent bacterial phyla was as follows: Plancomycetes (30%) > Proteobacteria (18%) > Acidobacteria (7%) > Bacteroidetes (10%) > Firmicutes, Verrucomicrobia, Chloroflexi (6%) > Actinobacteria (4%) > Gemmatimonadetes and Nitrospira (2%) (Fig. 1b).]

Prominent bacterial families between E- and E + soil were *Planctomycetaceae*, *Balstocatellaceae_(subgroup_4), Chitinophagaceae*, and *Bacillaceae* (Fig. 2). Moreover, we found several nitrogen-utilizing, phosphorus solubilizing, bio-controller, chitin degrading, nitrate reducers, drought and salt tolerant, other nutrients solubilizing bacterial families, for instance, *Planctomycetaceae, Xanthobacteraceae, Flavobacteriaceae, Bradyrhizobiaceae, Acidobacteriaceae_(Subgroup_1), DA101_soil_group, Anaerolineaceae, Nitrosomonadaceae, Tepidisphaeraceae, Gemmatimonadaceae, Cytophagaceae, Burkholderiaceae*, and *Comamonadaceae* (Fig. 2 and Supplementary Material 1). Endophyte-free tall fescue soil had higher *Planctomycetaceae* (31% of Planctomycetes) and *Chitinophagaceae* (10% of Bacteroidetes) compared to the E + soil where the *Balstocatellaceae_(subgroup_4)* (7% of Acidobacteria) and *Bacillaceae* (5% of Firmicutes) was higher (Fig. 2).

Soil Fungal Abundance, Diversity, and Community Composition

We identified 71 and 652 fungal ASVs in the E- and E + tall fescue soil collected from the tall fescue plots, respectively. In E + tall fescue soil, we identified 6 phyla, 24 classes, 43 orders, 76 families, and 112 bacterial genera. We identified 3 phyla, 6 classes, 10 orders, 18 families, and only 19 bacterial genera in E- tall fescue soil. In both E- and E + tall fescue soil, the dominant fungal phyla consisted of Basidiomycota and Ascomycota, respectively (Fig. 3a and 3b). Mean fungal Shannon diversity index was overall lower and was not statistically significant between the E- (mean H' = 1.21) and E+ (mean H' = 1.27) soil. Fungal beta diversity presented with principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarities showed no significant differences as well. Interestingly, however, we observed a fungal community change between E- and E + tall fescue soil. While Basidiomycota (70%) dominated E- soil, E + soil had Ascomycota as the prominent phylum (Fig. 3a and 3b). Based on the toxicity status of the endophyte presence in the tall fescue, E + soil showed a similar percent abundance at phyla level where both toxic and non-toxic infected tall fescue soil had Ascomycota as the prominent phylum (Fig. 4). Arbuscular mycorrhizal fungi (AMF) belonging to Glomeromycota phylum (1% of the total fungal abundance) were identified in only E + fescue soil (Fig. 3a). In the case of fungal genera, while E + soil had no such genus that exceeded more than 5% of the total abundance, the most prominent genus in E- soil belonged to

Cortinarius (59% of Basidiomycota) (Fig. 5). Interestingly, we measured greater diversity at the genus level in E + soil (111 genera) compared to E- soil (19 genera). These different fungal genera have been shown to contribute to plant growth promotion, plant-pathogen suppression, lignin degradation, nitrogen utilization, phosphorus solubilization, biodegradation, phytohormone production, provides resistance against abiotic stresses such as drought, salt intrusion, and cold tolerance, etc. (Fig. 5 and Supplementary Material 2).

Discussion

Despite the intricate nature of soil microbial populations, we found common patterns in bacterial community responses in the soil to the endophyte presence in tall fescue and our results from soil bacterial analysis indicate that the endophyte presence in tall fescue might have had a subtle effect on the bacterial community composition. Contrasting results, however, have been reported on the impact of the endophyte presence in grass species on soil microbial community composition and microbial functions. For instance, soil microbial communities may alter microbial functions due to aboveground endophyte infection of grass species, such as microbial carbon and nitrogen mineralization [25, 55–57]. Furthermore, endophyte infection of above-ground plant material stimulated below-ground microbial functions primarily due to endophyte-induced rhizodeposition [58]. In our study, the lack of bacterial diversity in community composition perhaps can be attributed to the soil micro-niche effect [59]. Due to the size of bacteria, they are expected to be in direct contact with their immediate surrounding, but often these micro-niches have a different composition from the soil matrix [60]; thus, plant roots may never come into direct contact with the bacterial communities living in these niches and perhaps never influencing the community composition of the bacteria living in soils [61].

In our study, Planctomycetes were the dominant oligotrophic phylum (r-strategists) found in both E + and E- tall fescue rhizosphere soil. It is typical to be adapted to nutrient-poor soil indicated by lower soil carbon and phosphorus [62–65], and they are thought to be crucial in soil organic carbon and complex carbon turnover, nitrogen cycle, and subsequently for soil nutrient availability [66–68]. The second dominant bacterial phylum for both E + and E- tall fescue soil was a versatile group of copiotroph known as Proteobacteria that responds to readily available carbon in soil [67, 69]. Additionally, these Proteobacteria follow a fast growth pattern in the soil which consequently may act as a plant growth promoter by releasing soil macro and micro-nutrients from organo-mineral complex [70, 71], especially under copiotroph environment [72]. It is well documented that E + tall fescue has a competitive advantage over E- grasses, particularly against climatic and edaphic stress, protection against herbivores, enhanced nutrient acquisition, especially, soluble P from nutrient-poor soils, and eventually rendering greater plant fitness [73–75] by producing metabolites of fungal-origin [73, 74]. In our study, another oligotroph microbial taxa, Acidobacter, was found in greater relative percent abundance in E + tall fescue rhizosphere soil which offers efficient carbon and nitrogen cycling from soil organic matter that can consequently be used as a readily available nutrient source for the E + plants [67, 76]. The Proteobacteria to Acidobacteria (P/A) ratio may serve as a general indicator of soil nutrient status; a low P/A ratio indicates oligotrophic soil environment and a high P/A ratio suggest nutrient richness [77]. In our study, the percent abundance

ratio of Proteobacteria/Acidobacteria (P/A) was lower in E + tall fescue rhizosphere soil (1.66) compared to E- tall fescue rhizosphere soil (2.57). E- tall fescue performs poorer in overall plant fitness and persistence [78], despite the higher soil nutrient status (indicated by high P/A), compared to E + infected fescue, possibly due to the lower percent abundance of the Acidobacter phylum. Additionally, known copiotrophs, such as Bacteroidetes and Verrucomicrobia were also present in relatively lower abundance, possibly, due to the overall lower nutrient concentration of the study site [79, 80].

In the case of fungal community composition in soil, endophyte presence in tall fescue showed a clear shift in fungal phyla in the rhizosphere. In agroecosystems, strong evidence of multilateral interactions between, plant population, soil fungi, and soil solution composition has been discovered [61, 81–83]. While the complex fungal community structure and greater diversity enable enhanced organic matter decomposition, thereby, promoting higher nutrient absorption by plants and accelerate soil nutrient cycling [84–86], the plants act as the energy source for the soil fungal population by releasing photosynthetic carbon and secondary metabolites in soil [87–91]. Thus, soil fungal diversity has a remarkable influence on the fitness of the plant population and soil nutrient composition [92, 93]. The prominent three fungal phyla in soil are the Ascomycota, Zygomycota, and Basidiomycota [81], and our study site was dominated by either Ascomycota or Basidiomycota depending on the presence of endophytes in tall fescue (not the type of endophytes). The measured lower SDI for the fungal population in the soil, both E + and E-, may be due to the overall higher soil pH of the study site; fungi generally grow better in acidic conditions [94], whereas, our study site had a mean soil pH of 6.5. The greater relative abundance of Ascomycota and Basidiomycota in E + and E- tall fescue rhizosphere soil, respectively, suggests that the presence of endophyte in tall fescue affects the rhizosphere fungal community structure possibly through a combination of i) alkaloids such as loline or peramine excretion in the host grass [95, 96], ii) production of VOCs and other biochemical induced by the tall fescue [97, 98] and finally, iii) higher rhizodeposition [99], all of which finally contribute to increased resource availability for soil fungi. This is, therefore, an indication of a three-way relationship between the plant (tall fescue), fescue dwelling fungal endophytes, and the soil fungal communities [100]. Furthermore, significantly greater plant-available P in E + soil compared to E- soil, particularly in non-toxic E + soil, suggests the unique contribution of a less studied novel endophyte-host associations to plant nutrition under limited soil plant-available P [101]. This plant-available P in the rhizosphere is likely to contribute to soil bacterial and fungal growth. Additionally, the combined presence of Ascomycota, Basidiomycota, and Glomeromycota in E + tall fescue soil, may further contribute to the promotion of plant growth [102]. A highly diverse soil microbial community can withstand the changing environment, show greater resilience, and may bring stability in ecosystem functioning [103–106]. The observed higher diversity of fungal genera in E + tall fescue soil is particularly important under a stressed environment where plant growth is affected and greater fungal genus presence in soil perhaps delivers greater stress amelioration [20, 107], against unusually higher atmospheric temperature experienced in the summer of 2019 before soil sampling for this study. Often, carbon acquisition can be strictly limited under abiotic stress such as drought and the plant-associated microbial communities lacks the necessary resources to sustain [108]. However, soil fungal communities may indirectly stimulate photosynthesis in plants by providing necessary nutrients

[109]. Thus, the presence of a complex fungal assemblage at genus level in E + tall fescue soil suggests that root excreted rhizodeposits from E + tall fescue into the soil may have enhanced the mobilization or recruitment of beneficial rhizosphere fungal communities, and in turn, these different soil fungal communities possibly could provide greater fitness and resilience to the plant [110–112]. In addition, a greater number of fungal genera in the soil is also important in offering higher functional redundancy for both “basic” and “rare” soil functions [113], particularly under disturbed environment, hence, the greater distribution of different functional groups is a clear indicator of greater functional redundancy [70] in E + soil compared to E- soil.

Conclusion

Our study suggests that a three-way mutualistic relationship exists between tall fescue, fungal endophyte, and the soil rhizosphere communities, particularly the soil fungal community. This study reveals that while there was a subtle change in the soil bacterial population-based on endophyte presence in aboveground tall fescue, prominent changes were observed in the fungal community at the genus level compared to the endophyte-free soil. These results point to the possibility that the different soil nutrient acquisition and environmental stress tolerance imparted by endophytes on tall fescue is probably the result of mobilization or recruiting of beneficial rhizosphere microorganisms, however, further field trials of different endophytes in common plant genetic backgrounds are needed to confirm this.

Declarations

Acknowledgments

The authors are grateful to the Center for Advanced Genetic Technologies, University of Georgia, and the Department of Crop and Soil Sciences, the University of Georgia for providing full support.

Funding

Funding was provided by The Center for Bioenergy Innovation, a US Department of Energy Research Center supported by the Office of Biological and Environmental Research in the DOE Office of Science

Author information

Affiliations

Kishan Mahmud

Center for Applied Genetic Technologies, University of Georgia, Athens, GA 30602, USA

Kendall Lee

Institute of Plant Breeding, Genetics and Genomics, University of Georgia, Athens, GA 30602, USA

Nicholas Hill

Department of Crop and Soil Sciences, University of Georgia, Athens, GA 30602, USA

Ali Missaoui

Center for Applied Genetic Technologies, University of Georgia, Athens, GA 30602, USA; Department of Crop and Soil Sciences, University of Georgia, Athens, GA 30602, USA; Institute of Plant Breeding, Genetics and Genomics, University of Georgia, Athens, GA 30602, USA

Contributions

Kishan Mahmud and Ali Missaoui: Conceptualization and Methodology.

Kishan Mahmud: Investigation, Analysis, Visualization.

Kishan Mahmud and Kendall Lee: Writing - original draft.

Ali Missaoui: Supervision, Writing and Revisions.

Nick Hill: Writing and Revisions.

Ali Missaoui: Funding acquisition.

The author(s) read and approved the final manuscript.

Corresponding author

Correspondence to Ali Missaoui.

Availability of data and material

The datasets during and/or analyzed during the current study available from the corresponding author on reasonable request

Ethics declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

1. Shantz H: **The place of grasslands in the Earth's cover.** *Ecology* 1954, **35:**143-145.

2. Dixon A, Faber-Langendoen D, Josse C, Morrison J, Loucks C: **Distribution mapping of world grassland types.** *Journal of biogeography* 2014, **41:**2003-2019.

3. Wedin WF: *Grassland: quietness and strength for a new American agriculture.* ASA-CSSA-SSSA; 2009.

4. Deng L, Shangguan Z-p, Sweeney S: **"Grain for Green" driven land-use change and carbon sequestration on the Loess Plateau, China.** *Scientific Reports* 2014, **4:**1-8.

5. Endale D, Schomberg H, Franzluebbers A, Seman D, Franklin D, Stuedemann J: **Runoff nutrient losses from tall fescue pastures varying in endophyte association, fertilization, and harvest management.** *Journal of Soil and Water Conservation* 2021, **76:**25-38.

6. Sala OE, Yahdjian L, Havstad K, Aguiar MR: **Rangeland ecosystem services: Nature's supply and humans' demand.** In *Rangeland systems.* Springer, Cham; 2017: 467-489

7. Zhao Y, Liu Z, Wu J: **Grassland ecosystem services: a systematic review of research advances and future directions.** *Landscape Ecology* 2020**:**1-22.

8. Leuchtmann A: **Systematics, distribution, and host specificity of grass endophytes.** *Natural toxins* 1993, **1:**150-162.

9. Field KJ, Pressel S, Duckett JG, Rimington WR, Bidartondo MI: **Symbiotic options for the conquest of land.** *Trends in ecology & evolution* 2015, **30:**477-486.

10. Bouton J, Gates R, Belesky D, Owsley M: **Yield and persistence of tall fescue in the southeastern coastal plain after removal of its endophyte.** *Agronomy Journal* 1993, **85:**52-55.

11. Young CA, Charlton ND, Takach JE, Swoboda GA, Trammell MA, Huhman DV, Hopkins AA: **Characterization of Epichloë coenophiala within the US: are all tall fescue endophytes created equal?** *Frontiers in chemistry* 2014, **2:**95.

12. Hoveland CS: **Importance and economic significance of the Acremonium endophytes to performance of animals and grass plant.** *Agriculture, ecosystems & environment* 1993, **44:**3-12.

13. Stuedemann JA, Hoveland CS: **Fescue endophyte: History and impact on animal agriculture.** *Journal of Production Agriculture* 1988, **1:**39-44.

14. Hunt MG, Newman JA: **Reduced herbivore resistance from a novel grass–endophyte association.** *Journal of Applied Ecology* 2005, **42:**762-769.

15. Parish J, McCann M, Watson R, Paiva N, Hoveland C, Parks A, Upchurch B, Hill N, Bouton J: **Use of nonergot alkaloid-producing endophytes for alleviating tall fescue toxicosis in stocker cattle.** *Journal of animal science* 2003, **81:**2856-2868.

16. Hill N, Bouton J, Hiatt E, Kittle B: **Seed maturity, germination, and endophyte relationships in tall fescue.** *Crop Science* 2005, **45:**859-863.

17. Wang H, Wang S, Wang R, Wang X, Li J: **Conservation tillage increased soil bacterial diversity and improved soil nutrient status on the Loess Plateau in China.** *Archives of Agronomy and Soil Science* 2020, **66:**1509-1519.

18. Koyama A, Wallenstein MD, Simpson RT, Moore JC: **Soil bacterial community composition altered by increased nutrient availability in Arctic tundra soils.** *Frontiers in microbiology* 2014, **5:**516.

19. Lehman RM, Acosta-Martinez V, Buyer JS, Cambardella CA, Collins HP, Ducey TF, Halvorson JJ, Jin VL, Johnson JM, Kremer RJ: **Soil biology for resilient, healthy soil.** *Journal of Soil and Water Conservation* 2015, **70:**12A-18A.

20. Porter SS, Bantay R, Friel CA, Garoutte A, Gdanetz K, Ibarreta K, Moore BM, Shetty P, Siler E, Friesen ML: **Beneficial microbes ameliorate abiotic and biotic sources of stress on plants.** *Functional Ecology* 2020, **34:**2075-2086.

21. Busby PE, Soman C, Wagner MR, Friesen ML, Kremer J, Bennett A, Morsy M, Eisen JA, Leach JE, Dangl JL: **Research priorities for harnessing plant microbiomes in sustainable agriculture.** *PLoS biology* 2017, **15:**e2001793.

22. Hinsinger P: **Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review.** *Plant and soil* 2001, **237:**173-195.

23. Akhtar MS, Oki Y, Adachi T: **Mobilization and Acquisition of Sparingly Soluble P-Sources by Brassica Cultivars under P-Starved Environment II. Rhizospheric pH changes, Redesigned Root Architecture and Pi-Uptake Kinetics.** *Journal of integrative plant biology* 2009, **51:**1024-1039.

24. Bertrand I, Holloway R, Armstrong R, McLaughlin M: **Chemical characteristics of phosphorus in alkaline soils from southern Australia.** *Soil Research* 2003, **41:**61-76.

25. Buyer JS, Zuberer DA, Nichols KA, Franzluebbers AJ: **Soil microbial community function, structure, and glomalin in response to tall fescue endophyte infection.** *Plant and Soil* 2011, **339:**401-412.

26. Iqbal J, Siegrist JA, Nelson JA, McCulley RL: **Fungal endophyte infection increases carbon sequestration potential of southeastern USA tall fescue stands.** *Soil Biology and Biochemistry* 2012,

44:81-92.

27. Matthews JW, Clay K: **Influence of fungal endophyte infection on plant–soil feedback and community interactions.** *Ecology* 2001, **82:**500-509.

28. Berg G, Smalla KJFme: **Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere.** 2009, **68:**1-13.

29. Rovira AJP, soil: **Root excretions in relation to the rhizosphere effect.** 1959, **11:**53-64.

30. Warembourg F, Paul EJP, Soil: **The use of C 14 O 2 canopy techniques for measuring carbon transfer through the plant-soil system.** 1973, **38:**331-345.

31. Jones DL, Hodge A, Kuzyakov YJNp: **Plant and mycorrhizal regulation of rhizodeposition.** 2004, **163:**459-480.

32. Marschner P, Neumann G, Kania A, Weiskopf L, Lieberei RJP, Soil: **Spatial and temporal dynamics of the microbial community structure in the rhizosphere of cluster roots of white lupin (Lupinus albus L.).** 2002, **246:**167-174.

33. Shi S, Richardson AE, O'Callaghan M, DeAngelis KM, Jones EE, Stewart A, Firestone MK, Condron LMJFme: **Effects of selected root exudate components on soil bacterial communities.** 2011, **77:**600-610.

34. Yang Y, Chen S, Wu X, Syed SI, Syed IUS, Huang B, Guan P, Wang D: **Grazing Affects Bacterial and Fungal Diversities and Communities in the Rhizosphere and Endosphere Compartments of Leymus chinensis through Regulating Nutrient and Ion Distribution.** *Microorganisms* 2021, **9:**476.

35. Franzluebbers A, Nazih N, Stuedemann J, Fuhrmann J, Schomberg H, Hartel PJSSSoAJ: **Soil carbon and nitrogen pools under low-and high-endophyte-infected tall fescue.** 1999, **63:**1687-1694.

36. Rudgers JA, Clay KJEL: **An invasive plant–fungal mutualism reduces arthropod diversity.** 2008, **11:**831-840.

37. Bergmann J, Weigelt A, van Der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM: **The fungal collaboration gradient dominates the root economics space in plants.** *Science Advances* 2020, **6:**eaba3756.

38. Hu L, Robert C, Cadot S, Zhang X, Ye M, Li B, Manzo D, Chervet N, Steinger T, Van Der Heijden M: **Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota. Nat Commun 9: 2738.** 2018.

39. Zhang J, Wang P, Xue K, Hao Y-b, Wang Y-f, Cui X-y: **Trait complementarity between fine roots of Stipa purpurea and their associated arbuscular mycorrhizal fungi along a precipitation gradient in Tibetan alpine steppe.** *Journal of Mountain Science* 2019, **16:**542-547.

40. Rana KL, Kour D, Sheikh I, Dhiman A, Yadav N, Yadav AN, Rastegari AA, Singh K, Saxena AK: **Endophytic fungi: biodiversity, ecological significance, and potential industrial applications.** In *Recent advancement in white biotechnology through fungi.* Springer; 2019: 1-62

41. Cameron DD, Neal AL, van Wees SC, Ton J: **Mycorrhiza-induced resistance: more than the sum of its parts?** *Trends in plant science* 2013, **18:**539-545.

42. Hacquard S, Kracher B, Hiruma K, Münch PC, Garrido-Oter R, Thon MR, Weimann A, Damm U, Dallery J-F, Hainaut M: **Survival trade-offs in plant roots during colonization by closely related beneficial and pathogenic fungi.** *Nature communications* 2016, **7:**1-13.

43. Frąc M, Hannula SE, Bełka M, Jędryczka M: **Fungal biodiversity and their role in soil health.** *Frontiers in Microbiology* 2018, **9:**707.

44. Daws SC, Cline LA, Rotenberry J, Sadowsky MJ, Staley C, Dalzell B, Kennedy PG: **Do shared traits create the same fates? Examining the link between morphological type and the biogeography of fungal and bacterial communities.** *Fungal Ecology* 2020, **46:**100948.

45. Etesami H, Alikhani HA, Hosseini HM: **Indole-3-acetic acid (IAA) production trait, a useful screening to select endophytic and rhizosphere competent bacteria for rice growth promoting agents.** *MethodsX* 2015, **2:**72-78.

46. Qiu W, Su H, Yan L, Ji K, Liu Q, Jian H: **Organic Fertilization Assembles Fungal Communities of Wheat Rhizosphere Soil and Suppresses the Population Growth of Heterodera avenae in the Field.** *Frontiers in plant science* 2020, **11:**1225.

47. Kour D, Rana KL, Yadav N, Yadav AN, Singh J, Rastegari AA, Saxena AK: **Agriculturally and industrially important fungi: current developments and potential biotechnological applications.** In *Recent advancement in white biotechnology through fungi.* Springer; 2019: 1-64

48. Kauppinen M, Saikkonen K, Helander M, Pirttilä AM, Wäli PR: **Epichloë grass endophytes in sustainable agriculture.** *Nature Plants* 2016, **2:**1-7.

49. Service NRC, Department A: *Keys to soil taxonomy.* Government Printing Office; 2010.

50. **<Procedure-Checklist-–-Amplification-of-Full-Length-16S-Gene-with-Barcoded-Primers-for-Multiplexed-SMRTbell-Library-Preparation-and-Sequencing.pdf>.**

51. Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP: **DADA2: high-resolution sample inference from Illumina amplicon data.** *Nature methods* 2016, **13:**581-583.

52. McMurdie PJ, Holmes S: **phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data.** *PloS one* 2013, **8:**e61217.

53. Erdem E, Erdogan H, Oztok U: **BIOQUERY-ASP: querying biomedical ontologies using answer set programming.** *Proc of RuleML2011@ BRF Challenge* 2011**:**573-578.

54. Nilsson RH, Larsson K-H, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D, Kennedy P, Picard K, Glöckner FO, Tedersoo L: **The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications.** *Nucleic acids research* 2019, **47:**D259-D264.

55. Franzluebbers A, Nazih N, Stuedemann J, Fuhrmann J, Schomberg H, Hartel P: **Soil carbon and nitrogen pools under low-and high-endophyte-infected tall fescue.** *Soil Science Society of America Journal* 1999, **63:**1687-1694.

56. Franzluebbers A, Hill N: **Soil carbon, nitrogen, and ergot alkaloids with short-and long-term exposure to endophyte-infected and endophyte-free tall fescue.** *Soil Science Society of America Journal* 2005, **69:**404-412.

57. Franzluebbers A, Stuedemann J: **Soil carbon and nitrogen pools in response to tall fescue endophyte infection, fertilization, and cultivar.** *Soil Science Society of America Journal* 2005, **69:**396-403.

58. Van Hecke MM, Treonis AM, Kaufman JR: **How does the fungal endophyte Neotyphodium coenophialum affect tall fescue (Festuca arundinacea) rhizodeposition and soil microorganisms?** *Plant and soil* 2005, **275:**101-109.

59. Vos M, Wolf AB, Jennings SJ, Kowalchuk GA: **Micro-scale determinants of bacterial diversity in soil.** *FEMS microbiology reviews* 2013, **37:**936-954.

60. Urbanová M, Kopecký J, Valášková V, Ságová-Marečková M, Elhottová D, Kyselková M, Moënne-Loccoz Y, Baldrian P: **Development of bacterial community during spontaneous succession on spoil heaps after brown coal mining.** *FEMS microbiology ecology* 2011, **78:**59-69.

61. Urbanová M, Šnajdr J, Baldrian P: **Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees.** *Soil Biology and Biochemistry* 2015, **84:**53-64.

62. Buckley DH, Huangyutitham V, Nelson TA, Rumberger A, Thies JE: **Diversity of Planctomycetes in soil in relation to soil history and environmental heterogeneity.** *Applied and Environmental Microbiology* 2006, **72:**4522-4531.

63. Chaudhry V, Rehman A, Mishra A, Chauhan PS, Nautiyal CS: **Changes in bacterial community structure of agricultural land due to long-term organic and chemical amendments.** *Microbial ecology* 2012, **64:**450-460.

64. Ditterich F, Poll C, Pronk GJ, Heister K, Chandran A, Rennert T, Kögel-Knabner I, Kandeler E: **Succession of soil microbial communities and enzyme activities in artificial soils.** *Pedobiologia* 2016, **59:**93-104.

65. Hartmann M, Frey B, Mayer J, Mäder P, Widmer F: **Distinct soil microbial diversity under long-term organic and conventional farming.** *The ISME journal* 2015, **9:**1177-1194.

66. Lupatini M, Korthals GW, de Hollander M, Janssens TK, Kuramae EE: **Soil microbiome is more heterogeneous in organic than in conventional farming system.** *Frontiers in microbiology* 2017, **7:**2064.

67. Fierer N, Bradford MA, Jackson RB: **Toward an ecological classification of soil bacteria.** *Ecology* 2007, **88:**1354-1364.

68. Chen Y, Xin L, Liu J, Yuan M, Liu S, Jiang W, Chen J: **Changes in bacterial community of soil induced by long-term straw returning.** *Scientia Agricola* 2017, **74:**349-356.

69. Ramirez-Villanueva DA, Bello-López JM, Navarro-Noya YE, Luna-Guido M, Verhulst N, Govaerts B, Dendooven L: **Bacterial community structure in maize residue amended soil with contrasting management practices.** *Applied Soil Ecology* 2015, **90:**49-59.

70. Mahmud K, Franklin D, Ney L, Cabrera M, Habteselassie M, Hancock D, Newcomer Q, Subedi A, Dahal S: **Improving inorganic nitrogen in soil and nutrient density of edamame bean in three consecutive summers by utilizing a locally sourced bio-inocula.** *Organic Agriculture* 2021**:**1-11.

71. Lugtenberg B, Kamilova F: **Plant-growth-promoting rhizobacteria.** *Annual review of microbiology* 2009, **63:**541-556.

72. Wang Q, Wang C, Yu W, Turak A, Chen D, Huang Y, Ao J, Jiang Y, Huang Z: **Effects of nitrogen and phosphorus inputs on soil bacterial abundance, diversity, and community composition in Chinese fir plantations.** *Frontiers in microbiology* 2018, **9:**1543.

73. Malinowski DP, Belesky DP: **Epichloë (formerly Neotyphodium) fungal endophytes increase adaptation of cool-season perennial grasses to environmental stresses.** *Acta Agrobotanica* 2019, **72**.

74. Wang J, Hou W, Christensen MJ, Li X, Xia C, Li C, Nan Z: **Role of Epichloë endophytes in improving host grass resistance ability and soil properties.** *Journal of Agricultural and Food Chemistry* 2020, **68:**6944-6955.

75. Malinowski DP, Belesky DP: **Adaptations of endophyte-infected cool-season grasses to environmental stresses: mechanisms of drought and mineral stress tolerance.** *Crop Science* 2000, **40:**923-940.

76. Eilers KG, Lauber CL, Knight R, Fierer N: **Shifts in bacterial community structure associated with inputs of low molecular weight carbon compounds to soil.** *Soil Biology and Biochemistry* 2010, **42:**896-903.

77. Joshi S, Jaggi V, Gangola S, Singh A, Sah V, Sahgal M: **Contrasting rhizosphere bacterial communities of healthy and wilted Dalbergia sissoo Roxb. forests.** *Rhizosphere* 2021, **17:**100295.

78. Waller JC: **Endophyte effects on cattle.** *Tall fescue for the twenty-first century* 2009, **53:**289-310.

79. Fierer N, Ladau J, Clemente JC, Leff JW, Owens SM, Pollard KS, Knight R, Gilbert JA, McCulley RL: **Reconstructing the microbial diversity and function of pre-agricultural tallgrass prairie soils in the United States.** *Science* 2013, **342:**621-624.

80. Trivedi P, Anderson IC, Singh BK: **Microbial modulators of soil carbon storage: integrating genomic and metabolic knowledge for global prediction.** *Trends in Microbiology* 2013, **21:**641-651.

81. Ding J, Jiang X, Guan D, Zhao B, Ma M, Zhou B, Cao F, Yang X, Li L, Li J: **Influence of inorganic fertilizer and organic manure application on fungal communities in a long-term field experiment of Chinese Mollisols.** *Applied Soil Ecology* 2017, **111:**114-122.

82. Mueller RC, Paula FS, Mirza BS, Rodrigues JL, Nüsslein K, Bohannan BJ: **Links between plant and fungal communities across a deforestation chronosequence in the Amazon rainforest.** *The ISME journal* 2014, **8:**1548-1550.

83. Sun R, Dsouza M, Gilbert JA, Guo X, Wang D, Guo Z, Ni Y, Chu H: **Fungal community composition in soils subjected to long-term chemical fertilization is most influenced by the type of organic matter.** *Environmental Microbiology* 2016, **18:**5137-5150.

84. Hiscox J, Savoury M, Müller CT, Lindahl BD, Rogers HJ, Boddy L: **Priority effects during fungal community establishment in beech wood.** *The ISME journal* 2015, **9:**2246-2260.

85. Kivlin SN, Winston GC, Goulden ML, Treseder KK: **Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales.** *Fungal Ecology* 2014, **12:**14-25.

86. Yao Q, Liu J, Yu Z, Li Y, Jin J, Liu X, Wang G: **Changes of bacterial community compositions after three years of biochar application in a black soil of northeast China.** *Applied Soil Ecology* 2017, **113:**11-21.

87. Ponge J-F: **Plant–soil feedbacks mediated by humus forms: a review.** *Soil Biology and Biochemistry* 2013, **57:**1048-1060.

88. Requena N, Jimenez I, Toro M, Barea J: **Interactions between plant-growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi and Rhizobium spp. in the rhizosphere of Anthyllis cytisoides, a model legume for revegetation in mediterranean semi-arid ecosystems.** *New Phytologist* 1997, **136:**667-677.

89. Sláviková E, Košíková B, Mikulášová M: **Biotransformation of waste lignin products by the soil-inhabiting yeast Trichosporon pullulans.** *Canadian journal of microbiology* 2002, **48:**200-203.

90. Van Bruggen AH, Semenov AM: **In search of biological indicators for soil health and disease suppression.** *Applied Soil Ecology* 2000, **15:**13-24.

91. Vázquez MM, César S, Azcón R, Barea JM: **Interactions between arbuscular mycorrhizal fungi and other microbial inoculants (Azospirillum, Pseudomonas, Trichoderma) and their effects on microbial population and enzyme activities in the rhizosphere of maize plants.** *Applied Soil Ecology* 2000, **15:**261-272.

92. Rousk J, Bååth E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, Knight R, Fierer N: **Soil bacterial and fungal communities across a pH gradient in an arable soil.** *The ISME journal* 2010, **4:**1340-1351.

93. Van Der Heijden MG, De Bruin S, Luckerhoff L, Van Logtestijn RS, Schlaeppi K: **A widespread plant-fungal-bacterial symbiosis promotes plant biodiversity, plant nutrition and seedling recruitment.** *The ISME journal* 2016, **10:**389-399.

94. Dix NJ: *Fungal ecology.* Springer Science & Business Media; 2012.

95. Guo J, McCulley R, Phillips T, McNear Jr D: **Fungal endophyte and tall fescue cultivar interact to differentially affect bulk and rhizosphere soil processes governing C and N cycling.** *Soil Biology and Biochemistry* 2016, **101:**165-174.

96. Lugtenberg BJ, Caradus JR, Johnson LJ: **Fungal endophytes for sustainable crop production.** *FEMS microbiology ecology* 2016, **92**.

97. Rostás M, Cripps MG, Silcock P: **Aboveground endophyte affects root volatile emission and host plant selection of a belowground insect.** *Oecologia* 2015, **177:**487-497.

98. Rasmussen S, Parsons AJ, Fraser K, Xue H, Newman JA: **Metabolic profiles of Lolium perenne are differentially affected by nitrogen supply, carbohydrate content, and fungal endophyte infection.** *Plant physiology* 2008, **146:**1440-1453.

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

100. Rojas X, Guo J, Leff JW, McNear DH, Fierer N, McCulley RL: **Infection with a shoot-specific fungal endophyte (Epichloë) alters tall fescue soil microbial communities.** *Microbial ecology* 2016, **72:**197-206.

101. Ding N, Guo H, Kupper JV, McNear Jr DH: **Phosphorus source and Epichloë coenophiala strain interact over time to modify tall fescue rhizosphere microbial community structure and function.** *Soil Biology and Biochemistry* 2021, **154:**108125.

102. Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Ruiz LV, Vasco-Palacios AM, Thu PQ, Suija A: **Global diversity and geography of soil fungi.** *science* 2014, **346**.

103. García-García N, Tamames J, Linz AM, Pedrós-Alió C, Puente-Sánchez F: **Microdiversity ensures the maintenance of functional microbial communities under changing environmental conditions.** *The ISME journal* 2019, **13:**2969-2983.

104. Griffiths BS, Philippot L: **Insights into the resistance and resilience of the soil microbial community.** *FEMS microbiology reviews* 2013, **37:**112-129.

105. Erkus O, De Jager VC, Spus M, van Alen-Boerrigter IJ, Van Rijswijck IM, Hazelwood L, Janssen PW, Van Hijum SA, Kleerebezem M, Smid EJ: **Multifactorial diversity sustains microbial community stability.** *The ISME journal* 2013, **7:**2126-2136.

106. Shade A, Read JS, Youngblut ND, Fierer N, Knight R, Kratz TK, Lottig NR, Roden EE, Stanley EH, Stombaugh J: **Lake microbial communities are resilient after a whole-ecosystem disturbance.** *The ISME journal* 2012, **6:**2153-2167.

107. Rho H, Hsieh M, Kandel SL, Cantillo J, Doty SL, Kim S-H: **Do endophytes promote growth of host plants under stress? A meta-analysis on plant stress mitigation by endophytes.** *Microbial ecology* 2018, **75:**407-418.

108. Taylor BN, Menge DN: **Light regulates tropical symbiotic nitrogen fixation more strongly than soil nitrogen.** *Nature Plants* 2018, **4:**655-661.

109. Kaschuk G, Kuyper TW, Leffelaar PA, Hungria M, Giller KE: **Are the rates of photosynthesis stimulated by the carbon sink strength of rhizobial and arbuscular mycorrhizal symbioses?** *Soil Biology and Biochemistry* 2009, **41:**1233-1244.

110. Van Der Putten WH: **Belowground drivers of plant diversity.** *Science* 2017, **355:**134-135.

111. Bever JD, Platt TG, Morton ER: **Microbial population and community dynamics on plant roots and their feedbacks on plant communities.** *Annual review of microbiology* 2012, **66:**265-283.

112. Lekberg Y, Bever JD, Bunn RA, Callaway RM, Hart MM, Kivlin SN, Klironomos J, Larkin BG, Maron JL, Reinhart KO: **Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence.** *Ecology Letters* 2018, **21:**1268-1281.

113. Yu J, Whalen JK: **A new perspective on functional redundancy and phylogenetic niche conservatism in soil microbial communities.** *Pedosphere* 2020, **30:**18-24.

Figures

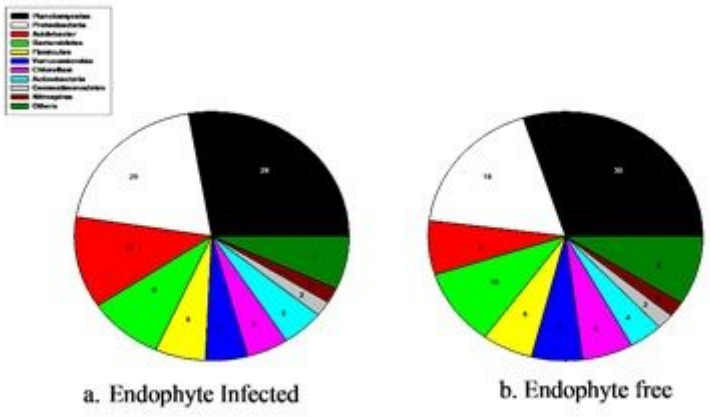

Figure 1

(a) and (b): Prominent bacterial phyla in soil based on endophyte presence in tall fescue

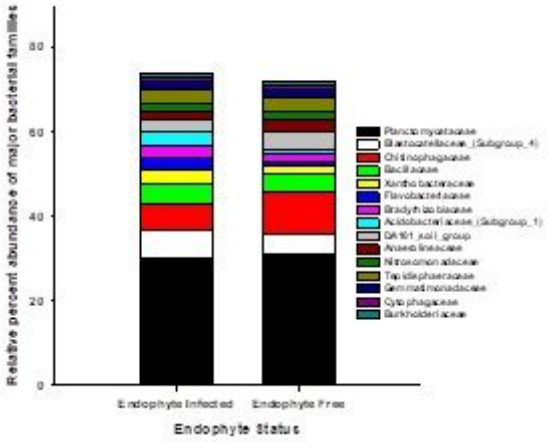

Figure 2

Percent abundance of major bacterial families in soil

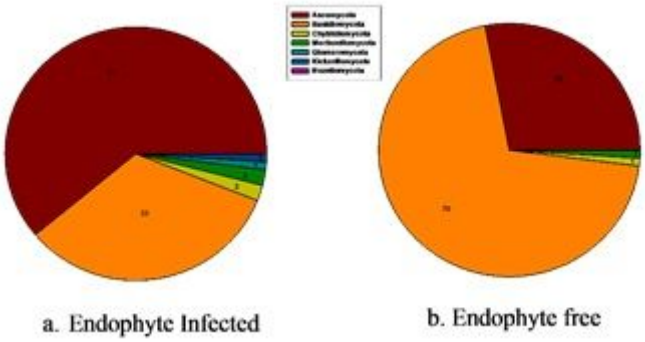

Figure 3

(a) and (b): Distribution of fungal phyla in soil based on endophyte presence in tall fescue

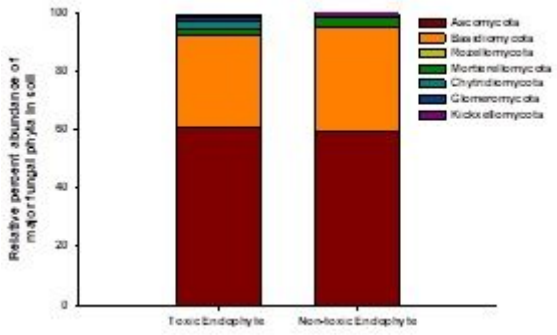

Figure 4

Prominent fungal phyla in soil based on endophyte toxicity in tall fescue

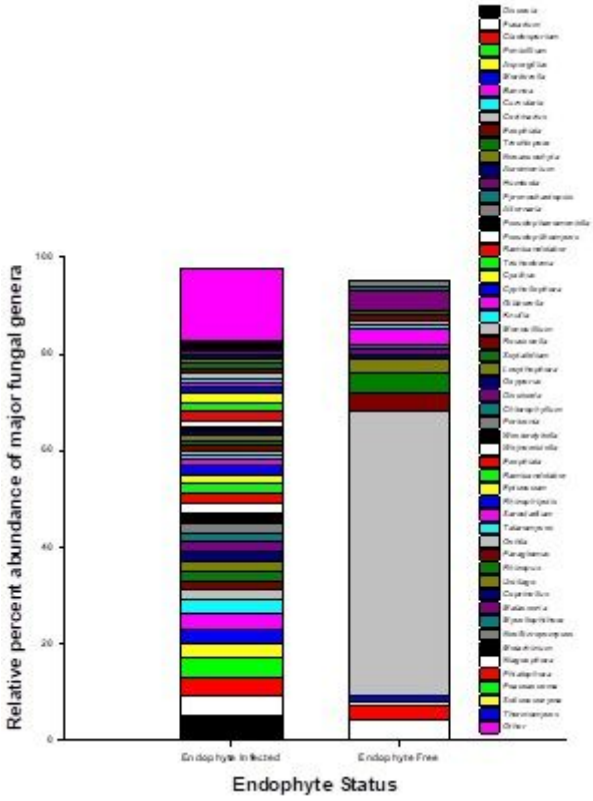

Figure 5

Percent abundance at genus level in soil (30 genera presented for E+ tall fescue soil)

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementalMaterial1.docx
- SupplementalMaterial2.docx