

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

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Research

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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 (°C), average soil temperature (0–15 cm) (°C), and average rainfall (mm) during summer months (June, July, and August) from 2015 to 2019.

Season	Maximum Atmospheric Temperature (°C)	Minimum Atmospheric Temperature (°C)	Daily Atmospheric Temperature (°C)	Daily Soil Temperature (°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 (AGRGGTYGATYMTGGCTCAG)/ 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 followed: 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/adaptor 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

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Contributions

Kishan Mahmud and Ali Missaoui: Conceptualization and Methodology.

Kishan Mahmud: Investigation, Analysis, Visualization.

Kishan Mahmud and Kendall Lee: Writing - original draft.

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Ali Missaoui: Funding acquisition.

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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.

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Figures

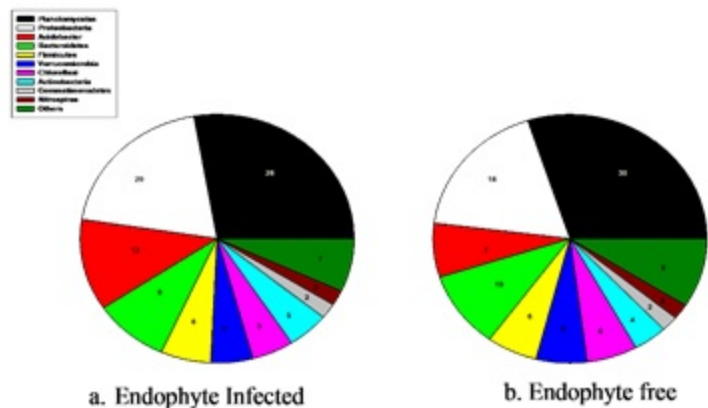


Figure 1

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

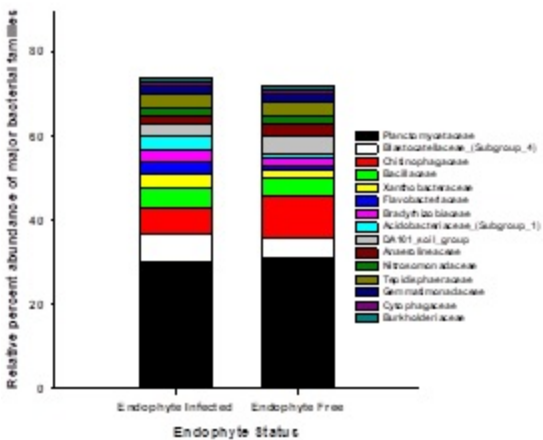


Figure 2

Percent abundance of major bacterial families in soil

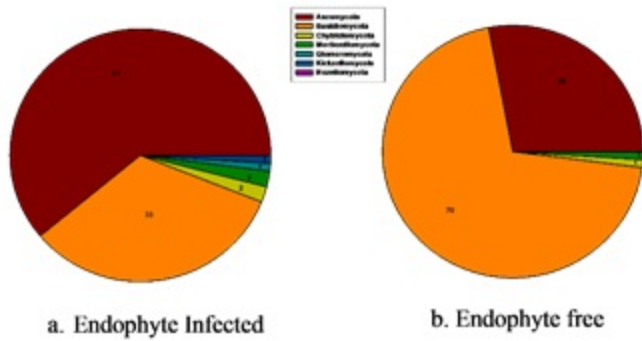


Figure 3

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

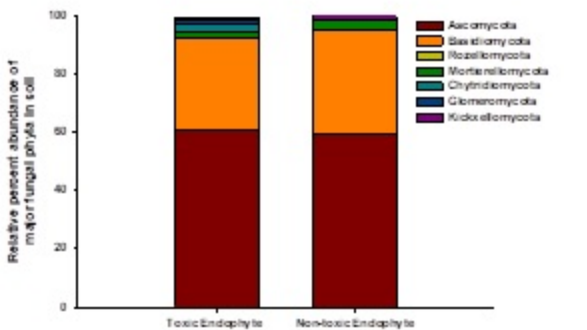


Figure 4

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

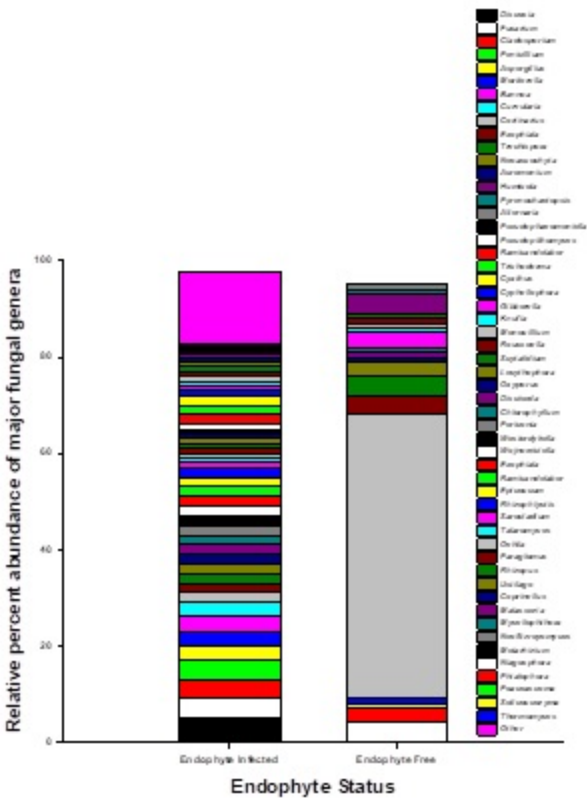


Figure 5

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

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