Plant Growth Promoting Fungal and Bacterial Endophytes of Tall Fescue: A Review

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Abstract

Plant growth promoting bacteria (PGPB) directly and indirectly influence the fitness of their host plants. While much of the work on plant growth promoting bacteria is from various plant rhizospheres, less is known about the strains that inhabit the internal spaces of plant tissues. Conversely, Clavicipitalean fungal endophytes of cool season grasses have been intensely investigated for the past few decades. Like plant growth promoting bacteria, the fungal endophytes also promote the health of their hosts. This paper highlights the current knowledge of plant growth promoting bacterial and fungal endophytes of tall fescue (*Lolium arundinaceum = Schedonorus arundinaceus = Festuca arundinacea*) which protect the plant from both abiotic and biotic stresses. Much of the work presented indicates just how little is known about the inter-relationships between the multiple endophytic microbial colonizers of turf grasses.

Introduction

Much of the current research in plant-microbe interactions is aimed at understanding the plant microbiome. The plant microbiome consists of the endophytic and epiphytic organisms that occupy the phyllosphere, rhizosphere, spermosphere, and seed. While pathogens are present, many of the microorganisms that colonize plants are plant growth promoting strains (PGPB), impacting the health of the host plant through production of phytohormones and antimicrobial compounds, solubilization and mobilization of mineral nutrients, nitrogen fixation, and nutrient uptake to name a few traits. Understanding the relationships between plants, plant growth promoting microbes, and commensals may help to determine the potential inoculum for effective biological controls or biofertilizers (microbial based fertilizers) which could serve as alternatives to chemical methods.

The term 'Endophyte' was first used in 1809 by the German botanist Henrich Friedrich Link to describe a group of quasi-parasitic fungal inhabitants of plants. Similarly, in 1866 de Bary used the term endophyte to define any microbe that lives in plant tissues[1]. Since then, endophytes of all microbial forms have been discovered. A more apt description would be to describe an endophyte as an asymptomatic microbial colonizer within host plant tissues[2–4].

Bacterial endophytes have been isolated from both warm and cool season grasses[4]. However, the mutualistic fungal endophytes of cool season grasses have been the most widely studied endophyte[5]. These fungi (Clavicipitaceae) gained notoriety due to their negative impact on grazing livestock. For instance, the United States beef industry faced significant economic losses caused from cattle grazing common toxic endophyte infected Kentucky 31 tall fescue[6–8] . Tall fescue, perennial ryegrass, and other cool-season pasture grasses can contain endophytic fungi capable of producing a variety of alkaloids in their host plants. When consumed, the alkaloid infused leaves result in a variety of aptly termed fescue toxicoses including 'ryegrass staggers' and 'sleepy grass syndrome'[9]. Additionally, afflicted animals can suffer from weight loss, reduced heat tolerance, and reduced fertility[10]. These adverse impacts led to greater interest in understanding the ecology of the fungal endophytes.

Epichloë spp. (family: Clavicipitaceae; phylum: Ascomycota; order Hypocreales) are one genera of the alkaloid producing fungi that infect cool season grasses[11]. These endophytes and their host plants are thought to be evolutionarily entwined, with the fungus perennating in the above ground tissues of the host. These asymptomatic biotrophs are confined to growth in the intercellular spaces of the above ground tissues of their hosts (Poaceae, subfamily Poöideae), and are notably absent from both the vasculature and the roots. However, structures such as mycelial nets have been documented on the leaf blades[12,13].

The fungi benefit from the relationship with the host as the endophytic habit allows for protection from environmental stresses like UV irradiation, or mycoparasites[14]. The fungal partner also benefits from a steady nutrient source from its autotrophic partner. An additional advantage to the fungal partner is from vertical transmission. In this process, the fungus infects the inflorescence primordia and perennates in the plant embryo, ultimately providing its offspring with a future mutualistic partner[15]. Importantly, hyphae of Epichloë do not impact seed viability even as they grow through the embryo and surrounding tissues[16]. Vertical transfer allows the fungal genotype and grass host linage to co-evolve in a conservative manner which is selective for host protection. Therefore, the continuous interaction between the fungal endophyte and host grass creates an interdependent mutualistic relationship[17].

Endophytic Colonization by Bacteria

Although vertical transmission is the norm for Epichloë endophytes, bacterial endophytes are typically horizontally transmitted. In fact, endophytic bacteria are known to be transient, and can go from the exterior portion of the plants to the interior at various points. Bacteria gain entry through natural openings such as hydathodes and stomata or cracks in lateral roots. In addition, bacterial endophytes can enter plants through wounds resulting from herbivory.

Entry via roots

According to Pinski et al., plant roots are the most common entry way for bacterial endophytes[18]. Their research group described five stages of endophytic colonization: 1) chemotaxis to root exudates; 2) adherence to rhizoplane; 3) formation of biofilm; 4) root surface penetration; and 5) internal colonization. Rhizodeposits consisting of exudates, mucilages, and sloughed cells attract bacteria to the rhizosphere, thus playing a role in the first stage of endophytic root colonization[19]. Successful microbial colonization of the rhizosphere is thought to be directly dependent on the ability to utilize the nutrients secreted by the plant[20]. Once established as part of the rhizosphere community, bacteria can become endophytes by achieving steps 2–5, entering through tears in the root surface. Endophytic bacteria colonize the root cortex or vascular tissues before making their way to the above ground tissue[21].

Root exudate compounds released by tall fescue contain a rich chemical diversity including sugars, phenolics, lipids and carboxylic acids. However, tall fescue infected with Epichloë coenophialum have a different root exudate composition than uninfected grasses[22]. One difference comes from fungal produced alkaloids. Loline alkaloids produce broad spectrum activity towards insect herbivores. Interestingly, lolines are produced at a significantly higher level than required to ward off insects, accumulate in the roots and are thought to contribute to the root exudate[23]. Our studies have shown that the alkaloid N-Formylloline (NFL) serves as a primary nutrient source for certain bacterial colonizers of Epichloë infected grasses[24]. Epichloë infection has been shown to contribute to microbial selection in the rhizosphere and phyllosphere through presence of NFL[24,25]. This selection of bacterial strains is believed to be based on their ability to catabolize lolines, as loline catabolizing strains showed a competitive advantage over non-catabolizing bacterial strains[24]. Thus, as the rhizosphere microbiome of tall fescue is influenced by plant exudates, the endophytic community drawn from the rhizosphere would be in part selected by the NFL secreted through the roots[25].

Additional root exudates found in grasses are phenylpropanoid anthocyanins and flavonoids. These were found to occur in statistically higher levels in Epichloë infected than in uninfected grasses[26]. This could have an impact on the bacterial populations as both chemicals have marked antimicrobial activity[27,28]. As these secondary metabolites have a rich carbon content composed of '15 Carbons, they could serve as significant nutrient sources for rhizosphere microorganisms. Plant growth promoting Pseudomonas putida PML2 catabolizes a wide range of flavonoids including flavonols, flavanones, flavones, and isoflavones[29]. Likewise, other rhizosphere bacteria including strains of Rhizobia and Bacillus have been shown to participate in the breakdown of flavonoids.

Azoarcus sp. BH72, Gluconacetobacter diazotrophicus, and some strains of Azospirillum spp. are present in roots, taking residence in the intercellular spaces. These bacteria have also been found in the culm and vessels of Kallar grass (Leptochloa fusca) and rice (Oryza sativa) with no strains living directly inside plant cells[30]. These three strains are thought to enter the plant either through wounds produced by helper microbes or through cracks adjacent to emerging lateral roots. They may enter the plant through undifferentiated root tips at the sites of elongation, which would allow the bacteria to access the developing stele before maturation of the endodermis. Azoarcus sp. BH72 also produces cellulolytic enzymes. However, these enzymes are bound to the cell surface rather than excreted and therefore likely assist this grass endophyte in colonizing the host with minimal harm[29].

Entry via seeds

The endospermosphere, or the internal tissue of the seed is dominated by the bacterial genera Agrobacteria, Bacillus, Burkholderia, Enterobacter, Paenibacillus, Pantoea, and Pseudomonas in a variety of plant hosts[31,32]. Our studies show that many of these bacteria also reside in tall fescue seeds[33]. As tall fescue seed is also host to E. coenophialum, bacterial colonizers would have to co-inhabit the seed with the fungal endophyte. Interestingly, our previous work demonstrated that there is less diversity in the endophytic bacterial populations of tall fescue seeds that are infected with Epichloë coenophialum versus endophyte free seeds[33]. Additionally, we found that fescue seeds are dominated by Pseudomonadaceae and Rhizobiaceae.

Entry via leaves

It is likely that part of the endophytic bacterial community arises from transient phyllosphere dwellers. These strains would likely enter the plant through the stomata, hydathodes or openings in leaf hairs. The phyllosphere is a difficult environment for individual cells, while the interior would be a respite from the abiotic stresses found on the leaf surface. Moreover, as tall fescue leaves infected with E. coenophialum have been found to secrete N-formylloline onto leaf surfaces, it is likely that the loline catabolizing strains that dominate the bacterial community on these leaves would be the primary endophytic colonizers from the leaf surface into the leaf[24].

Endophytic Proliferation

Avoiding plant defenses

Survival of endophytic microbes in the plant is highly dependent on plant defenses. Epichloë infection leads to down regulation of plant defense genes[26]. So, it may seem that fungal pathogens should easily infect the host grasses. However, the plants display increased chitinase gene expression. Epichloë spp. is thought to survive the chitinase through masking the cell wall chitin through small secreted proteins.

Bacterial endophytes presumably access plant interiors using the same points of entry as phytopathogens. However, the difference lies in the lessened defense response observed with non-pathogenic endophytes[1]. Bacterial endophytes avoid triggering host defense systems by maintaining low population size and are thought to produce less cell wall degrading enzymes than their pathogenic counterparts[34]. Additionally, flagella proteins which typically act as MAMPS are not recog-

nized during colonization by *Azoarcus* sp. BH72 which endophytically inhabits Kallar grass and rice[30]. *Bacillus subtilis* BSn5 was shown to mask its MAMP when grown as an endophyte of *Arabidopsis thaliana* by producing subtilomycin, a lantibiotic which binds to its own flagellin resulting in no flg22 induced immune response in the host[35]. *P. fluorescens* requires putrescine aminotransferase (SpuC) and a phosphodiesterase (MorA) to evade plant defenses through inhibition of pattern triggered immunity when endophytically inhabiting Arabidopsis[36]. These strategies may be used by strains of these bacterial endophytes that colonize turfgrasses.

Role of secondary metabolites

The relationship between the fungal endophyte and grass host is defined as a defensive mutualism, where fungal alkaloids maintain health of the host thereby benefiting the endophyte and plant. Epichloë endophytes produce alkaloids that belong to four chemical classes: ergot alkaloids, indole diterpenes, 1-aminopyrrolizidines and peramine[14]. It is believed that defense capabilities are only one of several ecological advantages of alkaloids[17]. At one point, scientists sought to remove fungal endophytes from pasture grasses because they were tainting the livestock food supply. Removal of endophytes to eliminate toxicosis resulted in poor health of the plant. Similarly, removal of bacterial colonizers from cool-season grasses such as tall fescue, perennial ryegrass, and annual bluegrass results in abnormal root development[37].

Secondary metabolites are thought to play a role in the communication between the fungal endophyte and grass host. Fungal produced alkaloids accumulate in the above ground tissue as well as in the seeds by the vertically transmitted endophyte. Further, alkaloid concentration varies within different plant tissues[38]. Thirty-eight host genes of *Lolium perenne* infected with *Epichloë festucae* var *lolii* were differentially expressed in infected versus endophyte free plants. For instance, pathogenesis related genes, including those involved in salicylic acid biosynthesis and signaling were downregulated[26]. This suggested a 'reprogramming' of the host metabolism leading to an increase in other secondary metabolites.

Another secondary metabolite produced by Epichloë endophytes are siderophores. *Epichloë festucae* makes the siderophores epichloënin A and ferricrocin[9,38]. Siderophores are primarily known for sequestering iron but are likely required for maintaining the mutualism between the fungus and the grass. The siderophores epichloënin A, epichloënin B, and ferriepichloënin A have been found in both endophyte-infected plants and endophyte mycelia[9,38–41]. Johnson et al., found that epichloënin deficient mutants overgrow and damage the host indicating that the siderophore plays a role in the plant-fungal mutualism[8]. Additionally, absence of siderophores has been linked to reduction of the ability of endophytic bacteria to detoxify active oxygen species which could limit survival in planta[18].

Potential Benefits of Bacterial Endophytes to the Host Plant

Plant growth promoting bacteria (PGPB) directly promote the growth of their hosts through traits such as nitrogen fixation, production of organic acids and siderophores, as well as production of various phytohormones and vitamins[42]. PGPB

also directly impact plant tolerance to abiotic and biotic stress by suppressing ethylene production via production of ACC deaminase, and the mobilization of essential nutrients like phosphorus and iron[43]. Indirectly, these bacteria prevent the growth of phytopathogens. This occurs through niche exclusion, production of antimicrobial chemicals and through the induction of plant defense mechanisms. The plant growth hormone Indole 3 acetic acid (IAA) functions to elongate plant cells. However, during cell elongation, carbon and other nutrients are thought to be released into the spaces occupied by endophytes. Therefore, this microbial produced chemical plays a dual role in the interaction between the endophytes and host[44]. Studies isolating bacterial endophytes in maize seeds show that most strains were able to fix nitrogen, solubilize phosphorus, produce antibiotics and the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase[45].

The culturable bacterial endophytes isolated and identified from *Festuca arundinacea* seeds possess putative traits linked to plant growth promotion and protection (Table 1). In a variety of other plants, these endophytic strains have demonstrated synthesis of IAA, ACC deaminase, siderophores, and phosphate solubilization[33,46,47]. While it is promising that the bacterial inhabitants of tall fescue seeds are known to have plant growth promoting traits, whether or not the same attributes occur in the grass requires additional study.

We cultured seven Bacillus species from fescue seed interiors. *Bacillus* sp. are known to produce the lipopeptides iturnin A and surfactin[48]. These surfactants have antimicrobial activity and have been shown to specifically suppress fungal pathogens. An endophytic *Bacillus* sp. has also been linked to induced systemic resistance of their hosts[4]. Another attribute associated with Bacillus strains is N fixation. This attribute of Bacillus could be important to grass hosts as NH^{4+} and NO^{3-} are limiting factors in turfgrass health[4]. Bacterial endophytes that produce nitrogenases have been shown to increase host plant biomass, outperforming rhizosphere dwelling N_2 fixing strains in helping host plants to survive in low nitrogen soils[30]. The low oxygen in the plant tissues provides a suitable environment for nitrogenase activity.

In addition, siderophore production was found in strains of endophytic *Bacillus pumilus* from Bermudagrass[4]. By sequestering iron, siderophores limit growth of potential pathogens. Other Bacilli isolated from the tall fescue seeds include *B. altitudinis* and *B. megaterium* which have been found to increase plant growth and produce ACC deaminase or boost amino acids and minerals in plants respectively[49]. In Arabidopsis, *B. megaterium* increases plant growth by way of cytokinin, auxin, and ethylene independent signaling[50,51]. *B. altitudinis* MS16 has been found to produce a lipopeptide biosurfactant and have antifungal activity towards the phytopathogens *Colletotricum gloesporioides* and *Sclerotinia sclerotiorum*[52].

Strains of *Bacillus toyonensis* and *B. safensis* were also isolated from tall fescue seed interiors. Endophytic, *B. toyonensis* COPE52 increased biomass and chlorophyll of the host while also showing antifungal activity against *Botrytis cinerea* in blueberry and tomato[53,54]. Additionally, endophytic *Bacillus safensis* ZXY16 produces siderophores, produces IAA, and perform phosphate solubilization[55].

We also isolated *Pantoea vagans* and *P. agglomerans* from interior portions of tall fescue seeds. These bacteria have demon-

Table 1. Putative plant growth promotion and protection properties from the listed bacteria which were isolated from surface-sterilized tall fescue seeds. Each strain of the culturable bacteria was identified through sequencing of 16S rRNA.

Culturable tall fescue endophytic seed isolates	IAA production	Synthesize ACC deaminase	Siderophore production	Nitrogen fixation	Phosphate solubilization	References
Bacillus altitudinis	X	X				[49]
Bacillus aryabhattai	X	X	X		X	[47]
Bacillus megaterium	X	X	X		X	[50]
Bacillus pumilus	X		X	X	X	[4]
Bacillus safensis	X	X	X		X	[55]
Bacillus sp.	X	X	X	X	X	[5, 42]
Bacillus toyonensis	X					[51, 52]
Pantoea agglomerans	X			X		[45]
Pantoea sp.	X		X		X	[45]
Pantoea vagans	X		X	X		[45]
Paenibacillus sp.	X		X	X	X	[32]
Pseudomonas flourescens	X		X		X	[60, 61]
Pseudomonas sp.	X		X	X	X	[60]
Pseudomonas syringae	X	X		X		[62]

strated phytohormone production in both wheat and rice, and have shown nitrogen fixation in tall fescue[32,45]. Thus, these species could be helpful during germination of tall fescue.

Plant associated fluorescent pseudomonads are well characterized for their plant growth promotion and protection traits. *Pseudomonas* sp. which was isolated from tall fescue seeds, are known to produce siderophores and indole-3-acetic acid (IAA) in some plants while also performing phosphate solubilization, and nitrogen fixation in others[56]. A strain of *P. syringae* was also found to reside in tall fescue grass seed interiors. This species has many pathogenic varieties but also has plant growth promoting strains such as *P. syringae* GR12-2 which is a nitrogen fixing symbiont of artic grasses[57]. Importantly, pseudomonads have been linked to induced systemic resistance in their plant hosts and produce antibiotics such as 2,4-diacetylphloroglucinol, phenazine, pyroolnitrin and pyoluteorin[58]. Similarly, pseudomonads are known to produce endochitinases and chitobiosidases which degrade cells of fungal pathogens[59]. As pseudomonads are abundant colonizers of tall fescue, it is likely that their plant growth promoting properties contribute to the fitness of these cool season grasses[58,59].

Future Studies and Current Challenges

The literature presented in this review highlights the current knowledge of the mechanisms that allow for attraction, mode of entry, and proliferation of bacterial grass endophytes. However, more work in this area is needed to fully understand the interplay between the plant and its fungal and bacterial endophytes. While the plant host provides nutrients and safe harbor from the environment, competition, or predation, the microbial endophytes provide the host protection from biotic and abiotic stresses. This protection results from the production of a variety of compounds that play multiple roles. Above all, understanding these roles could aid in manufacture of suitable biofertilizers for economically important grasses.

A microbial cocktail aimed to increase fitness of economically important grass types that don't naturally possess beneficial bacteria could be an alternative to chemical additives that may have environmental impacts. This could be of particular importance to grasses that lack Epichloë infection. Further, adding the bacteria apart from the fungal partner could allow for healthier grasses without the threat of toxicosis. Additionally, these investigations could uncover other issues in using certain bacteria as biofertilizers. For instance, even though some strains of *P. syringae* are plant growth promoting, others are important plant pathogens that use the plant growth hormone IAA as a virulence factor[57].

Our studies have only begun to take on the task of inoculating bacteria of interest into gnotobiotic tall fescue to determine the exact role of the bacteria in planta. Thus, additional studies are warranted to determine if exogenously applying microbial biofertilizers will assist in growth and protection of turfgrass hosts.

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Conflict of interest

The author declares that there is no conflict of interest.

Dates

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