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Review

Role of *Epichloë* Endophytes in Improving Host Grass Resistance Ability and Soil Properties

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ABSTRACT: The past decade has witnessed significant advances in understanding the interaction between grasses and systemic fungal endophytes of the genus *Epichloë*, with evidence that plants have evolved multiple strategies to cope with abiotic stresses by reprogramming physiological responses. Soil nutrients directly affect plant growth, while soil microbes are also closely connected to plant growth and health. *Epichloë* endophytes could affect soil fertility by modifying soil nutrient contents and soil microbial diversity. Therefore, we analyze recent advances in our understanding of the role of *Epichloë* endophytes under the various abiotic stresses and the role of grass−*Epichloë* symbiosis on soil fertility. Various cool-season grasses are infected by *Epichloë* species, which contribute to health, growth, persistence, and seed survival of host grasses by regulating key systems, including photosynthesis, osmotic regulation, and antioxidants and activity of key enzymes of host physiology processes under abiotic stresses. The *Epichloë* endophyte offers significant prospects to magnify the crop yield, plant resistance, and food safety in ecological systems by modulating soil physiochemical properties and soil microbes. The enhancing resistance of host grasses to abiotic stresses by an *Epichloë* endophyte is a complex manifestation of different physiological and biochemical events through regulating soil properties and soil microbes by the fungal endophyte. The *Epichloë*-mediated mechanisms underlying regulation of abiotic stress responses are involved in osmotic adjustment, antioxidant machinery, photosynthetic system, and activity of key enzymes critical in developing plant adaptation strategies to abiotic stress. Therefore, the *Epichloë* endophytes are an attractive choice in increasing resistance of plants to abiotic stresses and are also a good candidate for improving soil fertility and regulating microbial diversity to improve plant growth.

KEYWORDS: *Epichloë endophyte, abiotic stress, biochemistry mechanism, soil nutrient, soil microbes*

INTRODUCTION

In nature, plants form a beneficial relationship with microbes, including fungal endophytes, mycorrhizal fungi, and nitrogen-fixing bacteria, which can promote plant growth and adaptation to environmental stress.[1−3] The fungal endophytes of the genus *Epichloë* have provided new insights into changes of the phytochemistry and physiology of host grasses and the effects on the complex interactions occurring in the grassland ecosystem. *Epichloë* are a class of clavicipitaceous fungi that form a symbiotic relationship with grasses.[4,5] These *Epichloë* endophytes include the asexual species, previously referred to as *Neotyphodium* species, and the sexual *Epichloë* species.[5] The relationship between these fungal endophytes and host grasses is very complex, and understanding the nature of the association is essential for people involved with research into their ecological role and application in forage agriculture. Leaves of host grasses are symptomless; the hyphae are within all tissues of host grasses, except for the roots, and located in the intercellular spaces. The hyphae are attached to the cell walls of surrounding plant cells and absorb nutrients moving in apoplastic fluid. Importantly, the growth of hyphae is fully synchronized with the host grasses, with growth occurring when leaves and other tissues are being formed and ceasing when the surrounding tissue is mature.[6] However, the hyphae retain high metabolic activity until the surrounding tissue death.[7] A useful way to think about these fungal endophytes is that they grow and function as if they are a host tissue. Among their function in the plant is to synthesize protective compounds not produced by the host grass. The asexual species are exclusively transmitted in nature through the seed of the host plant (vertical transmission). Many of the sexual species are also vertically transmitted but have the potential to be horizontally transmitted. For horizontal transmission to occur, a switch in the regulation of the hyphae from being fully synchronized with the host grass to growth being ongoing occurs when inflorescence production commences.[6]

In current research, there are 29 recognized asexual *Epichloë* species, which transmitted to the next generation solely within host seeds, most of which are associate with a single host species.[8−10] There are currently 12 sexual *Epichloë* species, which are transmitted to new host plants through filamentuos ascospores, namely, horizontal transmission.[8,9,11] Symbioses of host grasses with *Epichloë* can be mutualistic or exhibit

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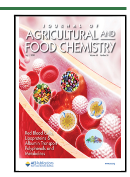

mutualistic characteristics.[12] In nature, these fungi are only found in symbiosis with cool-season grasses, and nearly all of these fungi can be cultured in culture medium. A method was reported by which novel associations between *Epichloë typhina* and *Festuca rubra* could be made by inoculating seedlings by inserting inoculum from cultures into a slit made at the growing point of axenically grown grass seedlings.[13] It has led to the production of selected combinations of grasses and *Epichloë* endophytes. Studies have shown that nearly all of the biologically significant properties of the *Epichloë* endophytes, including *Epichloë amarillans*, only occur when the fungi are growing biotrophically in host grasses.[14]

Over 40 years of study have revealed many effects that result from the presence of *Epichloë* endophytes in the important agricultural species, perennial ryegrass (*Lolium perenne*) and tall fescue (*Festuca arundinacea*). These include increased persistence of the host grasses as well as deleterious effects on grazing livestock.[15] However, ecologically important effects of *Epichloë* in other grasses, including *Achnatherum inebrians* and *Hordeum brevisubulatum*, in the vast grasslands of northwest China, are also becoming well-documented.[9] In particular, much of the studies about the effects of *Epichloë* endophytes on host grasses in China and, in particular, *A. inebrians* have focused on how their presence may enable the host grass to better tolerate abiotic stress, because *A. inebrians* plants are found in semi-arid grasslands, where the conditions are harsh and the soil fertility is low. Importantly, the presence of an *Epichloë* endophyte helps host grasses to better adapt to grassland ecosystems.

There are three predominant model relationships between *Epichloë* endophytes and host grasses: *Epichloë coenophiala*−*F. arundinacea* interaction, *Epichloë festucae* var. *lolii*−*L. perenne* interaction, and *Epichloë gansuensis*−*A. inebrians* interaction. The literature related to these endophyte/grass associations is dominated by studies on ryegrass and *F. arundinacea*; however, in recent years, there have been many studies on the effects of *Epichloë* endophytes on *A. inebrians* plants in China.[9] Interestingly, *Epichloë* endophytes can enhance the resistance of host grasses to abiotic stresses, and the implications of this in forage grazing systems has been well-documented with ryegrass and tall fescue.[15] With regard to abiotic stresses, increased resistance to salt stress,[16−21] drought stress,[12,22−34] waterlogging stress,[22,32,35,36] cold stress,[37,38] heavy metal stress,[29,39−42] and low nitrogen stress[43−46] and increased tolerance to combined stresses[29,47,48] have been reported when grasses are host to the endophytes of genus *Epichloë*. In addition, a number of studies have confirmed that the presence of an *Epichloë* endophyte could affect soil microbial communities and soil properties.[49−53] In addition, one study has demonstrated that *E. festucae* var. *lolii* induces alteration of hormone and defense protection in host perennial ryegrass.[54] *E. coenophiala* influences WRKY transcription factors of host plants, which may have effects on symbiotic stability.[55] With these beneficial functions, *Epichloë* endophytes influence the forage yield economic value in sown pastures and natural rangelands and open the possibilities of further benefits that could arise from studies to explore possible applications. Therefore, this review has provided a new perspective to understand the biochemical process of plant resistance to abiotic stress and improve soil fertility.

Research in the interactions of *Epichloë* and host grasses is providing a new understanding in the complex interactions that exist with grassland ecosystems, and this includes knowledge of the phytochemistry and physiology of host grasses. Importantly, the presence of an *Epichloë* endophyte increased the tolerance of host grasses to abiotic stresses and enabled host grasses to be better adapted to harsh environments in grassland ecosystems. Here, we summarize the biochemical mechanisms by which the presence of an *Epichloë* endophyte improves resistance of host grasses to abiotic stress and the biochemical process of improving soil fertility. The major points are that (1) the endophytes of the genus *Epichloë* improve the growth of host plants under drought stress, salt stress, heavy metal stress, waterlogging stress, cold stress, and low nitrogen stress and (2) the *Epichloë* endophyte−host grass symbiont improves soil properties and regulates soil microbial communities.

■ INFLUENCE OF *EPICHLOË* ENDOPHYTES ON HOST GRASS UNDER ABIOTIC STRESS

Drought Stress. During the life cycle of plants, they will be challenged by a great many environmental stresses, and drought stress negatively influences plant growth and limits crop production. However, plants respond to drought stress through physiological, biochemical, and morphological responses, culminating in stress tolerance. Many studies showed that the endophytes of the genus *Epichloë* play an important function in enhancing drought resistance in *Epichloë*-infected grasses through regulating the photosynthetic, osmotic adjustment, and antioxidant enzyme systems, water use efficiency, and nutrient accumulation.[12,22−34,56] Studies with *A. inebrians* have demonstrated that *E. gansuensis* infection (E+) increased proline accumulation and decreased superoxide dismutase (SOD) activity compared to plants without this *E. gansuensis* (E−) when under drought stress; however, photosynthetic capacity of E+ and E− *A. inebrians* plants does not differ when under drought stress.[57] The presence of an *Epichloë* spp. in *Elymus dahuricus* plants resulted in higher values in biomass, tiller numbers, and plant height under low soil moisture treatment than for endophyte-free plants, but no effects of the *Epichloë* spp. were observed in high soil moisture conditions.[58] In addition, under the low soil moisture treatment, E+ plants had higher antioxidative enzyme activity, such as for peroxidase (POD), SOD, ascorbate peroxidase (APX), and catalase (CAT), and higher proline content compared to E− plants; however, the H_2O_2 content of a plant host to an *Epichloë* spp. was lower than that for *Epichloë* spp.-uninfected *E. dahuricus* plants.[58] Therefore, the presence of this systemic endophyte promoted plant growth through improved antioxidative enzyme activity under the low soil moisture conditions.[58] Another study showed that the benefits of *Epichloë bromicola* to *Leymus chinensis* depended upon water availability. Further, the results indicated that total biomass was not influenced by the presence of the endophyte under well-watered conditions. Interestingly, the total biomass of E+ *L. chinensis* was higher than E− *L. chinensis*, regardless of fertilizer content under drought stress.[56] Further, it is reported that the beneficial effects of the presence of an *Epichloë* endophyte on *Achnatherum sibiricum* are dependent upon available resources; fertilizer addition resulted in greater beneficial effects of this endophyte on the growth of this species of grass. However, this advantage decreased under drought stress.[59]

Changes to the primary and secondary metabolism of both the *Epichloë* endophyte host grass have been reported when plants are exposed to high or low soil moisture contents and/or soil fertility. For example, the content of ergot alkaloids in tall fescue plant host to *Epichloë* sp. was enhanced under water

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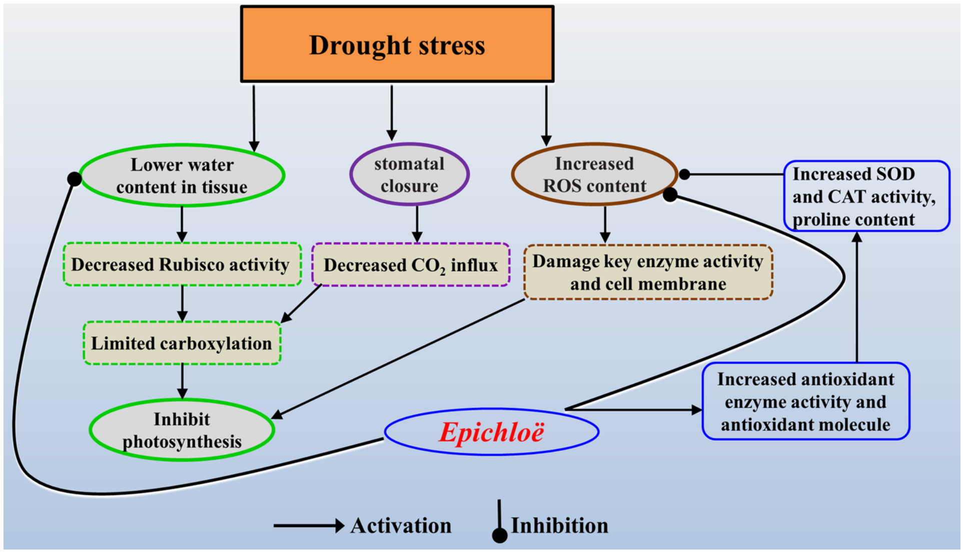

Figure 1. Schematic illustration of a proposed model to indicate that the *Epichloë* endophyte improves host grass growth by modulating photosynthesis of the host grass under drought stress. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

and/or nutrient treatments.[60] A recent study has shown that the presence of *E. gansuensis* enhanced water use efficiency and maintained the growth of *A. inebrians* plants under limit water availability environments by promoting nutrient absorption and improving photosynthetic efficiency.[34] The infection of perennial ryegrass plants with *E. festucae* strain Fl1 induced marked changes in three key areas, such as secondary metabolism, primary metabolism, and expression of stress-response genes; the endophyte also triggered metabolism reprogramming in host plants, especially secondary metabolism, and in addition, it also induced alteration in cell wall biogenesis and trichome formation.[61] The above results indicated that the endophyte enhanced resistance to drought. On the basis of these studies, we can confirm that endophytes of the genus *Epichloë* play a central function in increasing drought tolerance.

Drought stress increased ergovaline content in the pseudostem tissue of *Neotyphodium lolii*-infected *L. perenne* plants, and lolitrem B content in leaf blades and pseudostem tissue of genotype *L. perenne* G1146 plants enhanced with increasing drought stress.[62] Drought stress induces a range of physiological and molecular responses in plants, including photosynthesis repression[63] and stomatal closure.[64] Many genes were induced by drought stress, and these genes had been identified[65] and could be classified into two classes: (1) regulatory proteins that are involved in the expression of stress-responsive genes and (2) the function of proteins involved in abiotic stress tolerance.[66] Under drought stress, another study reported that water use efficiency was enhanced as a result of lowered water loss by reducing the leaf area and transpiration rate in a clover species (*Trifolium alexandrinum*).[67] Drought stress increased water use efficiency mainly as a result of a rapid decrease of stomatal conductance in *Pinus ponderosa* and *Artemisia tridentata*.[68] Therefore, the *Epichloë* endophytes probably increase water use efficiency of host grasses through decreasing stomatal conductance to increase plant tolerance to drought stress. One study demonstrated that drought stress inhibits photosynthesis by decreasing rubisco activity.[69] Drought stress inhibits the activity of the photosynthetic electron transport chain and decreases CO_2 availability in the chloroplast.[70] In leaves, the rubisco level is controlled by the rate of degradation and synthesis. Rubisco activity is regulated by the reaction with Mg^{2+} and CO_2 to carbamylate, a lysine residue in the catalytic site; photosynthesis declines rapidly; rubisco carboxylation decreased at a maximum velocity for ribulose-1,5-bisphosphate; and speed regeneration of ribulose-1,5-bisphosphate was slow in plants.[71,72] Therefore, *Epichloë* endophytes might improve the photosynthesis process to increase drought tolerance. In summary, the presence of an *Epichloë* endophyte might affect the photosynthetic system, osmotic system, antioxidant system, and water use efficiency of host grasses to increase drought tolerance. On the basis of the above results and our understanding, we propose a hypothetical model to explain the increasing resistance ability behavior of *Epichloë* endophytes in host grasses (Figure 1).

Salt Stress. The homeostasis of intracellular ion content is very important to the physiology of living cells. Generally, under salt stress, plants maintain low Na^+ levels and high K^+ levels in the cytosol, and a high K^+/Na^+ plays a central role to increase plant salt tolerance.[73] In this case, Na^+ accumulation is toxic and detrimental for plants, leading to compromised plant growth and metabolism through negatively influencing membrane stability, enzyme activity, and enhancing reactive oxygen species (ROS) production.[73] In the same condition, however, the presence of *Epichloë* endophyte provides a beneficial role to host grasses through modulating the nutrient stoichiometry, Ca^{2+} content, photosynthesis, chlorophyll content, nitrogen use efficiency, and nitrogen metabolism enzyme activity, leading to enhanced growth.[16,18−21] Among the findings linked to high-salinity conditions are that *Epichloë* spp.-infected (E+) plants had higher leaf survival rates of than plants without the endophyte at 170 mM NaCl, and the root dry matter of E+ plants was higher than that for E− plants. However, the presence of the *Epichloë* spp. did not affect shoot dry weight, and this leads to a lower shoot/root ratio in E+ plants compared to E− plants. Interestingly, *Epichloë* spp. infection decreased Cl^- and Na^+ contents in roots but enhanced the K^+ content of shoots. On the basis of these above results, it indicates that the endophyte improved host grass growth.[18] It was also reported that endophyte-infected

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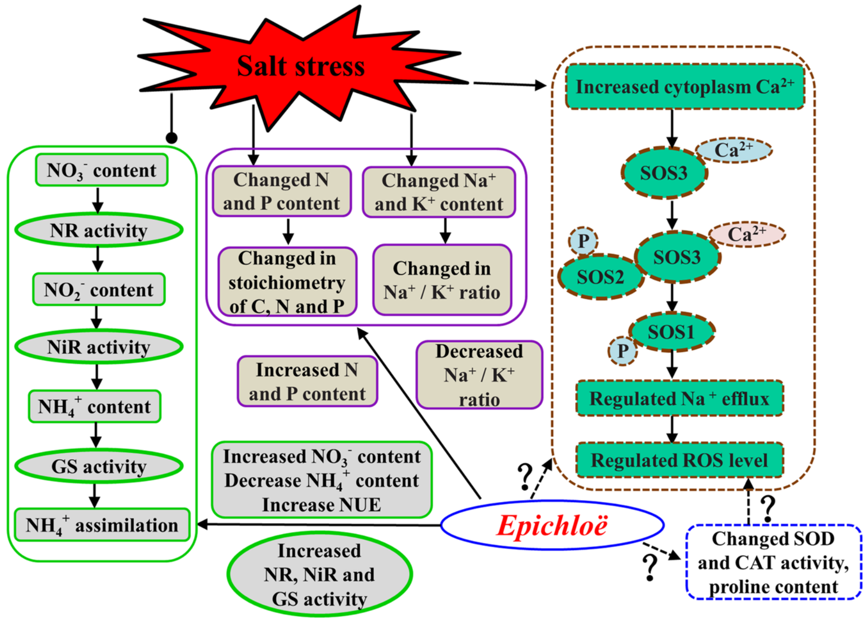

Figure 2. Schematic illustration of a proposed model to show that the roles of the *Epichloë* endophyte on increasing host tolerance to salt stress. NR, nitrogen reductase; NiR, nitrite reductase; GS, glutamine synthetase; and NUE, nitrogen utilization efficiency. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

grasses grow better than E− plants through increasing N, P, and K^+ contents and reducing Na^+ content; therefore, the endophyte modulates the stoichiometry to promote host grass growth under salt stress.[20] A recent study showed that the *Epichloë* endophyte improved the host growth through modulating the stoichiometry of C, N, and P, the contents of Ca^{2+}, Na^+, K^+, and chlorophyll, and photosynthesis.[16] Another study showed that *E. bromicola* increased the tolerance of *H. brevisubulatum* to salt stress by enhancing conversion of putrescine to spermidine and spermine.[17] Meanwhile, our studies showed that *E. gansuensis* increased salt tolerance of *A. inebrians* through enhancing nitrogen use efficiency, activity of nitrate reductase, nitrite reductase, and glutamine synthetase, and photosynthetic ability.[17] The above studies indicate that the *Epichloë* endophytes reduce toxicity of Na^+ and improve physiological processes of the host, therefore increasing salt tolerance in E+ grasses. The salt tolerance is closely related to ion homeostasis in a plant; therefore, using physiological and biochemical methods to maintain ion homeostasis through ion uptake, transport, and compartmentalization is not only an essential process for growth but is also crucial for normal plant growth during salt stress.[74,75] Regardless of their properties, in their cytoplasm, both halophytes and normal plants cannot tolerate high ion content; therefore, the excess poison ion is either sequestered in older tissues or transported to the vacuole, which is sacrificed, to protect plants from salinity stress.[73,76] The *Epichloë* endophytes may play a crucial role in maintaining ion homeostasis under salt stress, probably by regulating the function of salt-tolerance-related genes to increase plant tolerance. Many studies have demonstrated that the function of a salt overly sensitive (SOS) signal pathway is very important in salt tolerance and ion homeostasis.[77,78] Three important proteins, SOS1, SOS2, and SOS3, constitute the SOS signal pathway. The *Epichloë* endophytes may enhance the ability of host grasses to efflux Na, which helps to reduce the Na^+ content of the tissues. Research has shown that the *SOS1* gene encodes a plasma membrane Na^+/H^+ antiporter, which is important in modulating Na^+ efflux, and overexpression of the *SOS1* gene could increase plant tolerance to salt stress.[79,80] The *Epichloë* endophytes probably affect the function of the *SOS1* gene. The *SOS1* gene is also beneficial to long distance transport of Na^+ from belowground tissues to aboveground tissues. Interestingly, *Epichloë* endophytes are not present in the roots of host grasses, and therefore, how can *Epichloë* endophytes regulate *SOS1* gene expression in the different tissues of grasses? The *SOS2* gene encodes a threonine/serine kinase, and salt stress induces Ca^{2+} signals to activate the function of this gene, in which the C terminal of the SOS2 protein contains a NAF domain, as the function domain.[81] The *SOS3* gene encodes a myristoylated Ca^{2+}-binding protein, and the N terminus of SOS3 includes a myristoylation site, which plays a key role in plant salt tolerance.[82] The NAF domain of the SOS2 protein is an interaction site for the Ca^{2+}-binding domain of the SOS3 protein.[83] With the increase in the Na^+ levels of tissue, there is a dramatic enhancement in the intracellular Ca^{2+} concentration, which promotes it to bind with the myristoylated Ca^{2+} site of SOS3. The SOS2−SOS3 complex activated SOS1 protein phosphorylation, and the phosphorylated SOS1 protein can enhance Na^+ efflux,[84] reducing Na^+ toxicity for plants under salt stress. In addition, NADPH oxidases play a central role in ROS-dependent modulation of Na^+/K^+ homeostasis under NaCl stress.[85] The antioxidant system, including the non-enzymatic system and the antioxidant enzyme system, plays a crucial role in eliminating excessive ROS induced by NaCl stress. The NaCl tolerance of plant is positively correlated with the antioxidant enzyme activity, such as CAT, SOD, APX, glutathione reductase (GR), and guaiacol peroxidase (GPX). The NaCl tolerance of plants is positively correlated with the accumulation of antioxidant non-enzymatic compounds, such as phenols, proline, and reduced glutathione.[86,87] *Epichloë* may increase the antioxidant ability to increase plant tolerance to salt stress. In summary, *Epichloë* might regulate the SOS signal pathway, NADPH oxidases, and

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antioxidant system of host grasses to increase salt tolerance of a plant; therefore, we propose a hypothetical model to indicate how the *Epichloë* endophytes increase the tolerance of host grass to salt stress (Figure 2).

Heavy Metal Stress. It is generally known that heavy metal contamination is an urgent environmental problem and has a direct harmful impact on food and agricultural safety. Heavy metals are toxic for plants and interfere with plant physiological and biochemical processes, such as nitrogen and protein metabolism, nutrient uptake, respiration, and photosynthesis.[88] However, the *Epichloë lolii* endophyte provides an ability for host grass to adapt to heavy metal stress, and this increases the competitiveness of endophyte-infected plants over those lacking the systemic endophyte.[89] For example, *E. gansuensis*-infected *A. inebrians* plants had higher biomass, tiller numbers, and plant height compared to *A. inebrians* plants without this endophyte under 100 and 200 μM $CdCl_2$. In addition, the study showed that *E. gansuensis* increased antioxidative enzyme (CAT, APX, POD, and SOD) activity, H_2O_2 content, and chlorophyll *a* and *b* content but decreased proline and malondialdehyde contents compared to endophyte-free plants under 100 and 200 μM $CdCl_2$.[42] With perennial ryegrass, plants infected with endophyte accumulated more $CdCl_2$ than E− plants, especially in the shoots, and the presence of the endophyte increased tiller production and decreased leaf elongation under $CdCl_2$ stress. Further, $CdCl_2$ stress inhibited Fv/Fm, regardless of endophyte status.[40] The research showed that *Acremonium lolii*-infected perennial ryegrass showed higher values in tiller numbers than *A. lolii*-free plants. However, after 24 days of $ZnSO_4$ exposure, leaf water content and leaf fresh weights of ryegrass became suppressed and no advantage was conferred by *A. lolii* to its host.[39] *E. festucae* can enhance the tolerance of fine fescues to aluminum stress.[41] On the basis of this wide range of research, we could conclude that the presence of *Epichloë* mainly improved antioxidative enzyme activity, osmotic regulation, and photosynthetic capacity of host grasses, therefore enhancing heavy metal tolerance in E+ grasses. The effect of toxic heavy metals on plants is largely fast and strongly inhibits growth processes as well as decreased activity of the photosynthetic enzymes, correlated with senescence processes.[90,91] Heavy metal stress usually decreases chlorophyll synthesis as a result of the inhibition of enzymes for chlorophyll synthesis.[92] The study demonstrated that heavy metal stress can disturb electron flow through cytochrome b559 (cyt b559) of photosystem II (PS II) and the quinone acceptor sites of PS II; however, the possibility of the changes observed in photosynthesis and the synthesis of chlorophyll could be related to the influence of the *Epichloë* endophytes on the activity of the related enzymes. Also, photosystems can be inhibited by high ethylene content, increasing senescence processes under Cu stress conditions.[93,94] Ethylene may be involved in the Cu inhibitory action on plants.[95] Therefore, under heavy metal stress, *Epichloë* might regulate ethylene synthesis and signal to inhibit plant senescence, to increase heavy metal tolerance for host grasses. Cu stress increased the ethylene content through the increase of ACC synthase gene expression and activity.[96] The heavy metal stress can enhance the ethylene content, which increases lipoxygenase activity.[97] It was demonstrated that heavy metals induce lipoxygenase and the jasmonate pathway mediated ROS production; further, exogenous jasmonic acid (JA) enhanced ethylene content,[98] especially through regulating the activity of 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase and synthase.[99] One of the major results of heavy metal stress is increased ROS formation, which usually impairs the cellular components, such as nucleic acids, membranes, and chloroplast pigments.[100] It is possible that high NADPH oxidase activity can enhance H_2O_2 formation, further reducing cell wall extensibility.[101] The heavy metal stress also induces specific proteins, such as hydroxyproline-rich glycoproteins. After the hydroxyproline-rich glycoproteins are oxidated, the presence of excess H_2O_2 content toughened cell walls, inhibiting growth.[102] Therefore, the endophyte might eliminate excess ROS to protect host grass growth under heavy metal stress. On the basis of the above results and our understanding, we propose a hypothetical model to demonstrate how *Epichloë* endophytes can increase heavy metal tolerance of host grass (Figure 3).

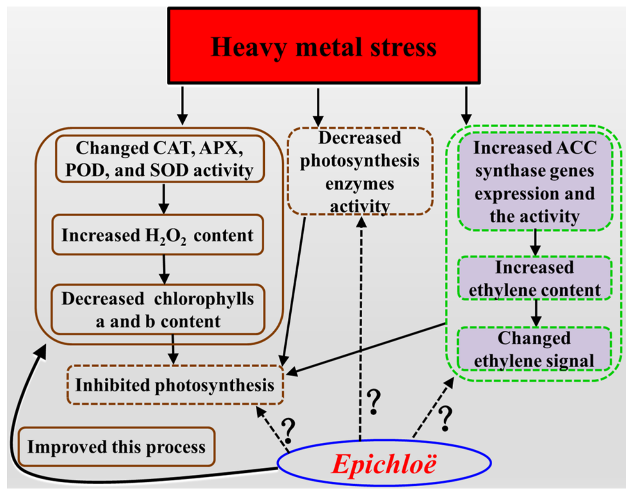

Figure 3. Schematic illustration of a proposed model to show the roles of the *Epichloë* endophyte on increasing host tolerance to heavy metal stress. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

Waterlogging Stress. Flooding often limits the yield of crops because it negatively affects plant growth.[103,104] Studies have been conducted that show that the presence of an *Epichloë* endophyte-enhanced waterlogging tolerance of host grasses. The presence of an *Epichloë* endophyte increased waterlogging tolerance in *H. brevisubulatum* by enhancing the chlorophyll content and the content of the osmoprotective proline and reducing electrolyte leakage and the MDA content, which suggests that the *Epichloë* endophyte had positively affected the oxidative balance and osmotic potential of the host grass. As a consequence, endophyte-infected plants had higher tiller numbers, shoots, and root biomass compared to endophyte-free plants.[36] A recent study has shown that waterlogging significantly inhibited the growth of *Festuca sinensis* plants; however, *Epichloë* endophyte infection significantly enhanced the root/shoot ratio and plant growth under these very wet conditions, evidence that, in at least some *Epichloë* endophyte grass associations, enhanced tolerance to waterlogged stress can occur.[32] Meanwhile, after harvesting tall fescue plants of a drought treatment trial, the regrowth following abundant watering was much greater with plants containing an *Epichloë* endophyte than with non-host plants.[22] In their natural environment, many plants are exposed to permanent or transient waterlogging. Flooding induces alterations in soil physiochemical properties, such as the

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oxygen content and redox potential. Therefore, plants growing under waterlogging stress face the stressful environment in terms of anoxia or hypoxia. The anoxia or hypoxia condition will continuously hamper plant growth and survival. Under a hypoxia environment, plants exhibit metabolic alteration from aerobic respiration to anaerobic respiration. O_2 deficiency generally leads to a decline of the net photosynthetic rate.[105] Waterlogging stress reduces transpiration and photosynthesis, which is a response to stomata closure.[106] Waterlogging stress induced the expression of some genes, which are involved with fermentative enzymes. Meanwhile, stomata conductance is hampered, and root hydraulic conductivity and net CO_2 assimilation rate are hindered. Furthermore, waterlogged conditions often lead to plants facing oxidative damage as a result of the generation of ROS. The waterlogging stresses decrease the water use efficiency, photosynthetic rate, and intrinsic water use efficiency of a plant.[106] Stomata modulation controls the CO_2 exchange rate under waterlogging stress.[105,106] In summary, the presence of an *Epichloë* endophyte might relieve the damage of anaerobic respiration and improve photosynthesis to promote host grass growth under waterlogging stress. Therefore, we propose a hypothetical model to demonstrate that the endophytes of genus *Epichloë* enhance the tolerance of host grasses to waterlogging stress (Figure 4).

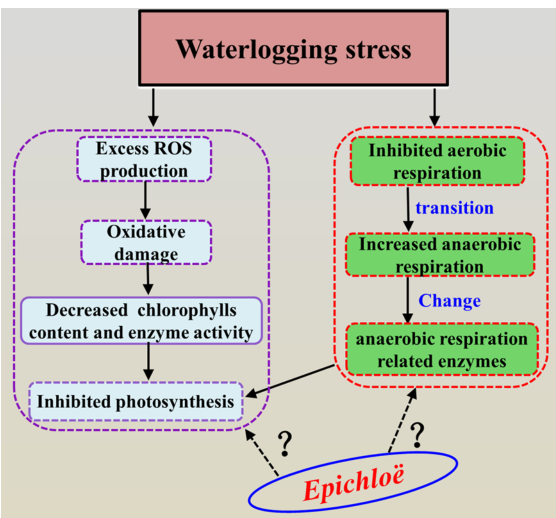

Figure 4. Schematic illustration of a proposed model to show the roles of the *Epichloë* endophyte on increasing host tolerance to waterlogging stress. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

Cold Stress. Cold stress adversely influences the growth and development of plants and significantly constrains the agricultural yield.[107] Increased cold tolerance in grasses that host an *Epichloë* endophyte has been reported in a small number of studies. One of the studies that reported enhanced cold tolerance as a result of the presence of an *Epichloë* endophyte was that of the germination of a seed of *A. inebrians*, where the presence of the *Epichloë* endophyte increased germination at temperatures less than 10 °C compared to a seed without the endophyte. Further, through transcriptional analysis, it is known that the regulation of some genes of E+ *A. inebrians* plants were changed, with 40 genes being downregulated and 112 genes being upregulated. Furthermore, some genes for which changes in regulation were observed were associated with the biosynthesis of unsaturated fatty acids and alkaloids and were associated with a low-temperature response.[37] It was also reported that the contents of total ergot alkaloids, ergonovine, and ergine were greater at 5 °C than at 22 °C in E+ plant; therefore, it showed that cold stress altered the content of the bioprotective ergonovine and alkaloid ergine.[38] Cold stress reduces the cell membrane fluidity as a result of alteration in lipid−protein composition and fatty acid unsaturation. The C-repeat binding factor/dehydration-responsive element binding (CBF/DREB) signal pathway is an important route for cold-responsive protein production, and the *cis*-acting element in CBF/DREB is dehydration-responsive element/C-repeat (DRE/CRT). The transcription factors bind to DRE/CRT sequences, namely, CBF/DREB1 in cold stress signaling, activating downstream gene expression, including second messengers, ROS, and mitogen-activated protein kinase (MAPK) cascade signaling.[108] Cold stress responses induced two-component histidine kinase, Ca^{2+} influx channels, and receptors associated with G proteins, which may be involved in a distinct route of the cold signal pathway.[109] Some cytoskeletal components regulate the Ca^{2+} channel activity of membrane rigidification to participate in cold sensing.[110] The role of the plasma membrane was considered as a site for the temperature perception.[111,112] The protein phosphorylation may provide a method to sense low temperatures in plants.[113] Next, most cascade signal pathways are induced, such as ROS, MAPK cascades, the activation of transcription factors, and Ca^{2+}-dependent protein kinases, which activate the expression of cold-responsive genes. The function of these genes is to control the cold stress signal transduction for increasing plant tolerance. Therefore, the endophyte could increase the expression of cold-responsive genes to enhance cold tolerance of host grasses. In summary, we propose a hypothetical model shown in Figure 5 to indicate that *Epichloë* endophytes increase cold tolerance of host grass.

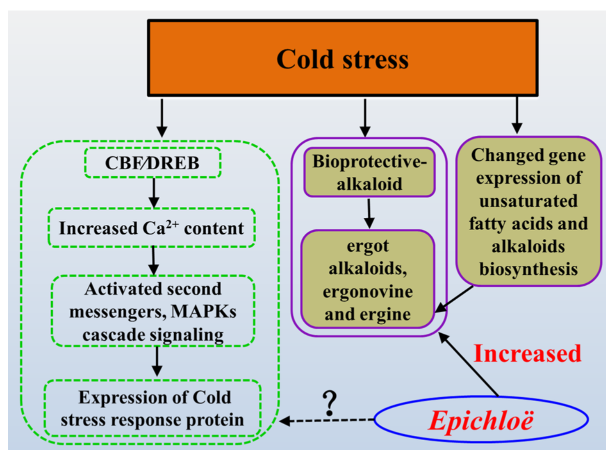

Figure 5. Schematic illustration of a proposed model to show the roles of the *Epichloë* endophyte on increasing host tolerance to cold stress. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

Low Nitrogen Stress. Nitrogen is one of the most important elements for plants; it influences plant growth and development and is a key factor for limiting crop quality and yield.[114] However, the application of excessive N fertilizer for crop production is causing serious environmental problems.[115] Therefore, understanding the low nitrogen tolerance mecha-

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nisms for plants is very important. Research shows that an *Epichloë* endophyte could increase the tolerance of *A. inebrians* plants to low nitrogen stress.[45−47] *E. gansuensis* improved ROS levels by regulating the G6DPH activity, glutathione (GSH) content, and NADPH/NADP$^+$ ratio. In addition, there were improvements in nitrogen use efficiency and the activity of enzymes involved with nitrogen metabolism under a low nitrogen environment, and thus, *E. gansuensis*-infected *A. inebrians* had higher contents of NO_3^-, NH_4^+, and nitrogen as well as higher biomass compared to endophyte-free plants.[45,46] In addition, it was reported that *Epichloë*-infected *A. sibiricum* had higher acid phosphatase activity and higher biomass compared to endophyte-uninfected plants under N+P− conditions; however, the presence of the endophyte slowly decreased the biomass through reducing leaf N content but distributed a higher N ratio to the photosynthetic system compared to E− plants under N−P+ conditions.[47] This change of N distribution significantly increased E+ plant biomass. In addition, it was reported that the interaction of *Epichloë*−*A. sibiricum* plant association is dependent upon P and N availability.[47] This study indicated that the endophyte infection enhanced the total biomass of host grasses, but the N source did not affect host grass growth. Interestingly, the endophyte enhanced nitrogen uptake compared to E− plant, although nitrogen use efficiency did not differ between E+ and E− plants.[44] These studies further confirmed that *Epichloë* endophytes play an important role in increasing low nitrogen tolerance in E+ grasses. It has also been shown that the gene AtNRT2.1 activates the nitrate transport activity under a low nitrate concentration.[116] Further, N starvation will highly reduce the expression of AtNRT2.4 and AtNRT2.5 in roots.[117−119] Next, nitrate reductase (NR) reduced nitrate to nitrite, and nitrite reductase (NiR) then further reduced nitrite into ammonium. Meanwhile, ammonium was converted from nitrate or directly from the soil and is assimilated through the glutamine synthetase (GS) and glutamine oxoglutarate amino-transferase (GOGAT) cycle. Glutamate dehydrogenase (GDH) catalyzes 2-oxoglutarate and glutamate, and this enzyme controls glutamate metabolism. Nitrogen use efficiency (NUE) plays a key role for plant growth under low nitrogen conditions; it was regulated by environmental and genetic factors. Our previous results showed that *E. gansuensis* increased NUE of a host grass under low nitrogen conditions.[46] Therefore, a combination of different strategies and approaches to achieve higher NUE is important for plants. The presence of an *Epichloë* endophyte could increase the activity of nitrogen metabolism enzymes and NUE to enhance low nitrogen tolerance of host grasses. In conclusion, we propose a model to demonstrate that the endophytes of genus *Epichloë* increase tolerance of host grasses to low nitrogen stress (Figure 6).

■ EFFECT OF *EPICHLOË* ENDOPHYTES ON SOIL MICROBIAL COMMUNITIES AND SOIL NUTRIENTS

Soil microbial communities play a central function in ecosystems; for example, in nutrient cycling, soil fertility, and plant yield.[120−122] The composition of the soil microbiome is affected by the interactions among soil, plant roots, and the environment, and in addition, plants profoundly influenced soil microbial communities.[123−125] A study indicated that the presence of *Epichloë coenophialum* can suppress the root knot nematode of tall fescue.[126] It was also reported that bulk soils and the rhizosphere soil associated with E+ and E− tall fescue

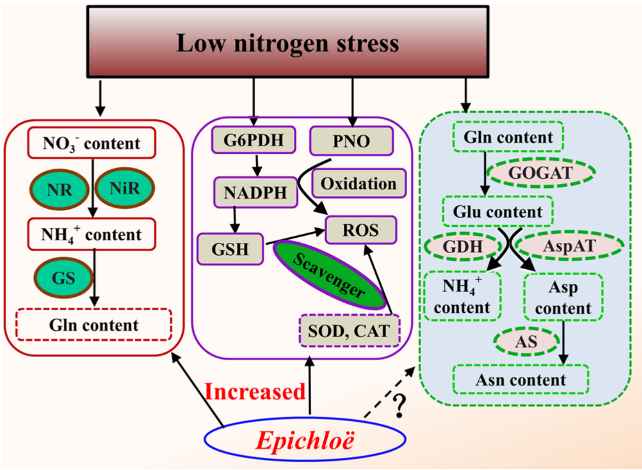

Figure 6. Schematic illustration of a proposed model to show the roles of the *Epichloë* endophyte on increasing host tolerance to low nitrogen stress. NR, nitrogen reductase; NiR, nitrite reductase; GS, glutamine synthetase; GOGAT, glutamate synthase; GDH, glutamate dehydrogenase; AspAT, asparagine transaminase; AS, asparagine synthetase, Gln, glutamine; Glu, glutamic acid; Asp, aspartic acid; Asn, asparagine; G6PDH, glucose-6-phosphate dehydrogenase; and PNO, NADPH oxidase plasma membrane. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

had different microbial communities; interestingly, although *E. coenophiala* infection clearly affected soil fungal communities, the effect of endophyte on prokaryotic communities was less pronounced.[52] In tall fescue, there was also evidence to indicate that *E. coenophialum* infection causes changes in the diversity and abundance of the soil microbe community.[49,127] The previous study confirmed that *E. coenophialum* infection caused small differences in soil microbial community diversity through the fatty acid methyl ester method.[49] Recently, under different growth conditions, *E. gansuensis* was found to influence root-associated fungal communities of *A. inebrians*.[53] In other studies, it demonstrated that soil total nitrogen and soil organic carbon at a depth of 0−20 cm soil under tall fescue (Kentucky-31) with high fertilization were greater with high than with low *E. coenophialum* infection; furthermore, soil total nitrogen and soil organic carbon were no different between high and low endophyte infection under low fertilization.[128] In addition, the study suggests that E+ tall fescue changed the soil organic carbon content through a decrease in soil microbial activity; short-term exposure of soil to detached E+ leaves compared to E− leaves decreased soil microbial biomass carbon and carbon mineralization but enhanced soil microbial biomass nitrogen and net nitrogen mineralization in the coarse fraction.[129] An earlier study of the effects of the presence of *E. coenophialum* on the soil demonstrated that the presence of the endophyte enhanced soil organic C and N contents compared to non-infected plants.[49] It was demonstrated that the soil of endophyte-infected tall fescue plots had higher soil organic carbon content compared to the soil of plots of endophyte-free plants.[130] Interestingly, it showed that the symbiosis of *E. coenophiala* and tall fescue affects soil C and N cycling, and there were significant endophyte treatment effects on several C and N fractions.[50] It has also been shown that the presence of *Epichloë uncinata* in meadow fescue (*Festuca pratense*) did not influence the soil content of C and N; however, the contents of NH_4^+ and NO_3^- were different between the E+ and E−

plots.[131] *E. coenophialum*-infected tall fescue contains alkaloids not found in endophyte-free plants, and the presence of these secondary metabolites may be one possible factor for differences in the soil content of N and C.[132,133] *Epichloë* spp.-infected tall fescue plants contain loline alkaloids, which influenced epiphytic bacterial microflora of tall fescue.[134] The composition of tall fescue rhizosphere microbial communities had been shown to clearly differ between E+ and E− tall fescue plants, which suggested that the presence of *Epichloë* spp. affects the microbial community structure.[135] It is possible that loline alkaloids produced by a small number of *Epichloë* spp. in host grasses influence rhizosphere microbial communities.[135] Recently, the study described that that the fungal endophytic communities of tall fescue green leaves are strongly influenced by *Epichloë*, but the endophytic bacterial community structures of tall fescue green leaves are unaffected by *Epichloë*.[136] The endophytic bacterial community of E+ tall fescue seeds had lower diversity compared to E+ tall fescue seeds, which showed that *E. coenophiala* influenced the seed microbial community.[137] Studies have indicated that secretion of metabolites by roots potentially alter the microbial community structure of the rhizosphere.[138,139] On the basis of these reports, it was confirmed that the endophytes of genus *Epichloë* had an important ecological function for improving soil microbial communities and soil nutrients, and we propose a model to show that the endophyte of the genus *Epichloë* improves soil nutrients and influences the microbial community structure (Figure 7).

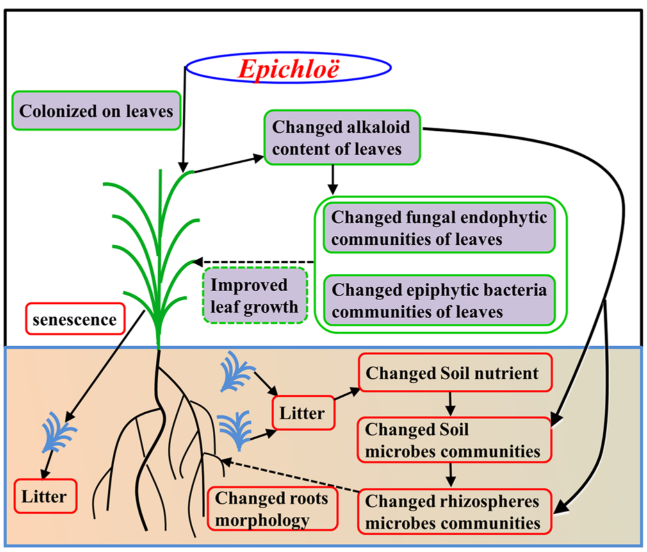

Figure 7. Schematic illustration of a proposed model to show the roles of the *Epichloë* endophyte on improving soil fertility and soil microorganisms. Solid line, it has been confirmed by experiments; dotted line, it has not been confirmed by experiments.

PROSPECTS

There are increasing numbers of researchers focusing on the resistance of host plants of the *Epichloë* endophyte to abiotic stresses or the impacts of *Epichloë* endophytes on soil nutrients and soil microorganisms. In the present review, we verified the biological roles of *Epichloë* endophytes in host grasses to abiotic stresses and soil properties. During the 40 years of research on the symbiotic relationship of *Epichloë* endophyte−host grass, much research has focused on environmental stresses and few studies have focused on soil properties. We propose that higher tolerance of E+ host plants to abiotic stresses and the improvement in soil properties by the presence of *Epichloë* endophytes should be acknowledged in the breeding strategy. In addition, we can learn more about the biochemical mechanisms of how the presence of an *Epichloë* endophyte increases abiotic stress resistance of host grasses, and with this beneficial knowledge, breed new varieties of grasses using these *Epichloë* endophytes. In the future, we believe that researchers will make breakthroughs in these and related areas and will use a combination of different techniques to clarify that endophytes can improve the resistance of their hosts. Microbiome, metabolomics, soil science methods, and especially molecular biology will be used to clarify how endophytic fungi can improve the biochemistry mechanisms of the host for drought resistance, salt resistance, heavy metal resistance, cold resistance, low nitrogen resistance, and waterlogging resistance, which will provide the basis for improving land use efficiency and ensuring food safety.

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Jianfeng Wang, Zhibiao Nan, and Wenpeng Hou designed the experiment. Jianfeng Wang, Michael J. Christensen, Zhibiao Nan, Wenpeng Hou, Xiuzhang Li, and Chao Xia wrote the paper. Chunjie Li and Wenpeng Hou checked the paper.

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Notes

The authors declare no competing financial interest.
‡Michael J. Christensen: Retired scientist.

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