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REVIEW

Epichloë (formerly *Neotyphodium*) fungal endophytes increase adaptation of cool-season perennial grasses to environmental stresses

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Abstract

Many cool-season grass species have evolved with asexual, nonsymptomatic fungal endophytes of the genus *Epichloë* (formerly *Neotyphodium*) of the family Clavicipitaceae. These associations range from parasitic to mutualistic and have dramatic effects on grass host chemistry, increasing resistance to abiotic (drought, soil mineral imbalance) and biotic (vertebrate and invertebrate herbivory, nematodes, plant pathogens, plant competition) stresses. Native endophyte strains produce a range of bioprotective alkaloid and other nonalkaloid secondary compounds, several of them known to have detrimental effects on grazing animals. In the past two decades, epichloid endophyte strains have been selected with marginal or no capacity of producing ergot and/or lolitrem alkaloids. These novel endophyte strains have been introduced to several grass cultivars with the idea to increase grass host resistance to abiotic stresses without hindering grazing livestock, and abiotic stresses to ensure high competitive ability of symbiotic grass cultivars. In this presentation, we discuss mechanisms underlying the competitiveness of epichloid endophyte/grass associations and consequences of endophyte infection for grassland ecosystem functions.

Keywords

alkaloids; competition; environmental stresses; *Epichloë* endophytes; grassland ecosystems; abiotic stress; mineral stress

Introduction

Plant communities, including grasslands ecosystems, form an array of relationships with microorganisms. Many of these interactions are mutualistic and result in significant advantages of symbiotic plants in terms of abiotic and biotic stress tolerance over their nonsymbiotic counterparts. The most successful examples are the N₂-fixing symbioses [1] and arbuscular mycorrhizas [2]. In both cases, host plants are able to use more efficiently mineral nutrients from nutrient-deficient soils. As a result, such symbiotic plants have higher competitive ability and can dominate the ecosystems [3,4].

Several members of the genus *Epichloë* (formerly *Neotyphodium*) [5] of the family Clavicipitaceae have been identified as common fungal endophytes of some important cool-season forage grasses, such as tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh.] (syn. *Festuca arundinacea* Schreb.) [6], perennial ryegrass (*L. perenne* L.) [7], and meadow fescue [*L. pratense* (Huds.) Darbysh.] (syn. *F. pratensis* Huds.) [8]. These symptomless endophytes, also referred to as epichloid endophytes [9], are asexual

interspecific hybrids that colonize intercellular spaces of grass shoot meristems and basal parts of leaf sheaths, and are transmitted vertically via grass seeds [10,11]. The endophyte of tall fescue, *E. coenophiala*, is phylogenetically described as a triparental hybrid with inferred ancestral progenitors from *E. festucae*, *E. typhina* subsp. *poae*, and the *Lolium-associated* endophyte (LAE) [10,12]. In summer-dormant, Mediterranean morphotypes of tall fescue [13], two additional unnamed endophyte species, designated FaTG-2 and FaTG-3, have been identified [14,15]. These endophytes have also been characterized as interspecific hybrids between *E. festucae* and an unidentified *Lolium-associated* endophyte [12,16] and they differ from *E. coenophiala* in morphology, chemotype, isozyme profiles, alkaloid composition, and microsatellite markers [14–16]. *Epichloë uncinata*, the endophyte of meadow fescue, is a hybrid between *E. bromicola* and *E. typhina* subsp. *poae* [17]. The endophyte of perennial ryegrass, *E. festucae* var. *lolii*, is a haploid, nonhybrid strain [10]. Epichloid endophytes are also common in other cool-season grasses, i.e., hair-grass (*Deschampsia* spp.), colonial bent (*Agrostis capillaris* L.), orchardgrass (*Dactylis glomerata* L.), couch grass (*Elymus repens* L.), timothy (*Phleum pratense* L.) [18], and *Elymus* spp. from Western China [19].

The mutualistic interactions between epichloid endophytes and grasses are highly integrated involving morphological, physiological, biochemical, immunological, and life cycle traits of the partners to increase the fitness of the symbiota [17,20]. It is not well understood how the fungal and plant organisms interact to recognize each other and suppress defense responses that otherwise would prevent the establishment of harmful fungal infections in the host grass [21,22]. Malinowski and Belesky [23,24] speculated that grass plants could recognize the presence of epichloid endophytes as shown by increased production of chitinase, resveratrol, and phenolic compounds in response to infection. Recent research has evidenced that a recognition of the fungal endophyte (described as “cross-talk”) does occur through channels of communication between a grass host and its endophyte within the symplast [25]. Numerous studies have confirmed that production of phenolic compounds and other antioxidants is higher in endophyte-infected than noninfected grasses and it facilitates, among other responses, the ability of host grasses to cope with antioxidative stress [23,26–28].

Tall fescue, meadow fescue, perennial ryegrass, and other fescues are also known to be hosts to nonepichloid symptomless fungal endophytes, including *Phialophora*-like and *Gliocladium*-like (Deuteromycetes) fungi [29,30], often referred to as p-endophytes. A third group of nonepichloid endophytes consists of parasitic *Acremonium* species similar to *Neotyphodium chilense*, an endophyte of orchardgrass (*Dactylis glomerata*) [31]. These parasitic endophytes are referred to as a-endophytes. The *Phialophora*-like and *Gliocladium*-like endophytes are closely related [30]. The seed-borne *Phialophora*-like endophytes have been reported in tall and meadow fescue [29,32]. *Gliocladium*-like endophytes have been reported in perennial ryegrass and they can sporulate on the host plant [33]. Artificial infection of tall fescue and perennial ryegrass plants with *Gliocladium*-like endophytes resulted in a significant increase in peroxidase activity in leaf sheaths [34]. This indicates that *Gliocladium*-like endophytes can trigger a systemic defense mechanism, a response typical for infection with parasitic fungi. Both epichloid endophytes (e-endophytes) and p-endophytes often occur cosymbiotically [29,35]. The ecological role of p-endophytes is unknown. In agar culture, *Phialophora*-like endophyte of tall fescue expresses activity against a wide spectrum of fungal pathogens of grasses [36]. In meadow fescue, infection with a p-endophyte either decreased shoot dry matter (DM) in field-grown plants [32] or increased it in plants grown under controlled growth conditions [37]. The effects of e-endophytes and p-endophytes on root DM and physiological parameters in drought-stressed meadow fescue were opposite, suggesting that p-endophytes might benefit plants under optimal soil water conditions [37]. The parasitic a-endophytes are found in Italian ryegrass (*L. multiflorum*) and *F. paniculata*, and their ecological and physiological role is not understood [38].

In this review, we discuss recent findings on adaptations of cool-season grasses and their mutualistic *Epichloë* fungal endophytes to a range of environmental stresses and underlying physiological and biochemical mechanisms.

Alkaloid metabolites produced by epichloid endophyte–grass host associations

Although symbioses between asexual epichloid endophytes and cool-season grasses can range from antagonistic to mutualistic [17], there is a strong evidence for selective advantage of endophyte-infected grasses in native and improved grasslands [39,40]. Increased competitive ability of endophyte-infected grasses is the combination of altered growth and reproduction characteristics, and tolerance to a range of abiotic and biotic stresses [23], resulting in modifications of grassland ecosystem functions [22,41,42]. The direct basis for modifications of competitive ability of grass host may be numerous alkaloid and nonalkaloid secondary metabolites produced either by the endophyte themselves or by the grass hosts in response to infection [24,43,44]. The most known alkaloid metabolites are ergot, loline, peramine, and peramidine alkaloids because of their detrimental effects on herbivory by vertebrates and invertebrates [43]. The enzymatic pathways for synthesis of these alkaloids are regulated entirely by the fungal genome [45–47]. Within endophyte/grass host combinations, alkaloid profiles are determined by the fungal species and strains. The amounts of produced alkaloids depend on the hypha concentration in the plant, the plant species and genotype, tissue or organ, and environmental conditions (water and mineral nutrient availability, temperature) [22,48–53]. Nonalkaloid metabolites identified in endophyte-infected grasses include sesquiterpenoids, fatty acids, and phenolic compounds occurring in timothy (*Phleum pratense* L.) infected with *E. typhina* [54–56]. Flavonoids have been detected in bluegrass (*Poa ampla* Merr.) infected with *E. mollis* (Morgan-Jones & W. Gams) Leuchtm. & Scharld [formerly *N. typhinum* (Morgan-Jones & W. Gams) Glenn, C. W. Bacon & Hanlin] [57]. The ecological significance of these compounds in terms of biotic stress tolerance of endophyte-infected grasses is unknown.

Ergot alkaloids

Ergot alkaloids (clavines, lysergic acid and its amides, and ergopeptines) were the first endophyte-mediated metabolites associated with toxicity to animals grazing on endophyte-infected grasses [58,59]. Lysergic acid derivatives may cause psychedelic effects [60], whereas ergonovine and ergotamine are known to cause vasoconstrictive effects [61]. Agroclavine has antimicrobial activity [62]. Ergovaline is effective against insects and mammals [63–65]. Ergot alkaloids produced by clavicipitaceous fungal endophytes can cause toxicosis to animals grazing on infected grasses, e.g., summer slump and fescue foot [63,66]. The summer slump syndrome occurs during hot weather periods and may be manifested through symptoms such as hyperthermia, agalactia, reduced reproductive capability and retention of the winter coat. The fescue foot syndrome manifests usually during cold weather conditions causing dry gangrene of limbs and extremities.

Loline alkaloids

Loline alkaloids (*N*-acetyllooline, *N*-formyllooline) are synthesized by tall fescue and meadow fescue infected with *E. festucae* [67, 68] or *E. uncinata* [69] endophytes, respectively, and by perennial ryegrass infected with *E. festucae* var. *lolii* at elevated temperatures [70]. When compared with ergot or lolitrem alkaloids, loline alkaloids have negligible effects on livestock performance [71], despite their much higher concentrations in endophyte-infected grasses than those of other alkaloids [36,72]. Loline alkaloids are potent insecticides [73] with a mode of action similar to that of nicotine [74].

Pyrrrolizidine alkaloids

Peramine is a pyrrolopyrazine alkaloid. In contrast to the other alkaloids produced by the endophyte–grass associations, it is a single metabolite [75]. Peramine has no known effects on mammal herbivores [76] and functions as an anti-invertebrate defensive metabolite by deterring feeding of a range of insects [77,78].

Diterpene alkaloids

Lolitrems are the most known indole diterpene alkaloids with antivertebrate properties [79]. Lolitrems are produced only by the perennial ryegrass–*E. festucae* var. *lolii* associations [80], although some strains of *E. festucae* var. *lolii* are incapable of producing lolitrems in the grass host. The most common response of vertebrates to lolitrem B are tremors and staggers [81]. Epoxy-janthitrems are a group of five compounds also belonging to the indole diterpene alkaloids [82]. The epoxy-janthitrems have only been detected in perennial ryegrass infected with the novel endophyte strain AR37 of *E. festucae* var. *lolii* [83]. Epoxy-janthitrems are toxic to adult African black beetle (*Heteronychus arator*) [84], larvae of Argentine stem weevil larvae (*Listronotus bonariensis*) [85], root aphid (*Aploneura lentisci*) [86] and porina larvae (*Wiseana* spp.) [87].

Nonalkaloid secondary metabolites

Nonalkaloid secondary metabolites, i.e., sesquiterpenoids, fatty acids, phenolic compounds, and flavonoids have been isolated from several grass hosts infected with epichloid endophytes [57,88,89]. These metabolites have been shown to have antimicrobial [88], antioxidant [23,28], and pest-deterrent properties [90].

Ecological advances of endophyte-infected grasses

Systemic, endophytic fungi have been found in 20–30% of all grass species [91]. Symptomless, mutualistic epichloid fungal endophytes have been shown to dramatically alter morphological, physiological, and chemical attributes of their host grasses resulting in improved tolerance of symbiotic plants to a range of abiotic [23,92] and biotic stresses [93]. Ultimately, such adaptations enable endophytic grasses to be more competitive against noninfected counterparts (intraspecific competition) and other plant species (interspecific competition), and more persistent in a range of environments [41,94].

Mechanisms of endophyte-induced tolerance to biotic stresses

Vertebrates. The most beneficial attribute contributing to the dominance of endophyte-infected grasses in native and managed ecosystems is likely the ability of symbiotic plants to produce a range of alkaloids and nonalkaloid secondary metabolites protecting them from herbivores, nematodes, pathogenic fungi, and neighboring plants [95]. Clay and Schardl [72] postulated that alkaloids produced by endophyte-infected grasses are the primary determinant of antiherbivore effects and not the history of grass species domestication. As indicated earlier, ergot and lolitrem alkaloids are very efficient weapons against defoliation by vertebrate animals. Numerous reports confirm that endophyte-infected grasses are rapidly increasing their geographic range and frequency across diverse environments. The antiherbivory effects of endophyte-infected grasses has been evidenced in domesticated [58,96] and indigenous livestock [97–99]. Wild herbivores, i.e., voles (*Microtus* sp.), rabbits (*Oryctolagus* sp.), Canada geese (*Branta canadensis*), grasshoppers (Orthoptera: Acrididae), and ants (Hymenoptera: Formicidae) are also negatively affected by endophyte-infected grasses and prefer to graze on noninfected plants [100–103] or feed on noninfected seed [104,105]. Ergot alkaloids are suggested to reduce population densities of some root-knot [106] and migratory nematodes [107,108], although another mechanism of nematode deterring is also proposed in endophyte-infected grasses [109]. In contrast, novel endophytes that are lacking the ability to produce ergot alkaloids in associations with tall fescue grass host have no effect on nematode populations [110].

Invertebrates. It has been evidenced that approximately 45 insect species belonging to 10 families are susceptible to alkaloids produced by endophyte-infected grasses [25]. The most toxic alkaloids to insects are loline and peramine [96,111]. Interestingly,

symbiotic grasses can dramatically increase the production of lolines in response to leaf damage by insects or mammal herbivores [67,112]. Some insects, i.e., Argentine stem weevil (*Listronotus bonariensis*), a major pasture pest in New Zealand, are extremely sensitive to peramine [111]. Others, like aphids (Hemiptera: Aphididae), may differ in their response to particular grass–endophyte combinations that can determine a specific alkaloid profile [68,113]. Results of numerous studies suggest that the antagonist effects of epichloid endophyte-infected grasses on invertebrates may be more pronounced in agronomic than native grasses [114]. This may be a result of greater variation in infection rates, alkaloid production and profiles, and host and endophyte genotypes in agronomic compared with native grass species. Lehtonen et al. [115] observed that with increasing mineral nutrient availability in soils, bird cherry aphid (*Rhopalosiphum padi*) herbivore performance decreased on perennial ryegrass plants in response to infection with *E. festucae* var. *lolii*. The authors postulated that loss of endophyte infection after long coevolutionary relationship might critically reduce grass plant competitiveness in regard to herbivory resistance. Endophyte infection of grasses cannot only affect the performance of herbivorous insects, but also their predators. For example, Finkes et al. [116] found a significant decline in spider family richness in field dominated by endophyte-infected tall fescue plants when compared to fields containing endophyte-free plants and this phenomenon was not related to the abundance of the prey insects.

Plant pathogens. One of the ecological advances of endophyte-infected grasses is protection against some plant pathogens [117]. Such plant pathogens inhibition properties have been documented in pure endophyte cultures [36,118] and in symbiotic plants. In response to endophyte infection, tall fescue was more resistant to seedling blight caused by *Rhizoctonia* spp. [119] and crown rust caused by *Puccinia coronata* [120]. Similar protection against fungal pathogens was reported in ryegrass [121], *Panicum agrostoides* infected by the endophyte *Balansia henningsiana* [122], timothy infected by an *Epichloë* sp. endophyte [123], and other native grasses [124]. In some endophyte/grass associations, however, the effects on pathogen resistance were neutral or negative [6,125].

Aphids are known to be vectors of numerous viruses, including barley yellow dwarf virus, one of the most harmful cereal viruses [126]. Reduction in aphid populations on endophyte-infected tall fescue and meadow fescue can significantly reduce incidence of this virus [127,128]. Interestingly, epichloid endophyte of grasses can harbor a number of mycoviruses that cause no apparent symptoms on infected plants [129,130]. Their role in the endophyte-grass host associations is not known.

Interactions with arbuscular mycorrhizal fungi. Grasses often form mutualistic associations with arbuscular mycorrhizal (AM) fungi. Mycorrhizal endophytes affect many physiological processes in grass hosts that help the plants efficiently take up P and other minerals, increase drought tolerance, resistance to some pathogens, and increase their competitive ability [131]. Exudation of organic compounds in the rhizosphere by epichloid endophyte-infected grasses (see section “Mineral imbalance stress”) can alter the mutualistic symbioses among the grass hosts and AM fungi [132]. In agronomic grasses, i.e., tall fescue, and annual and perennial ryegrass, endophyte infection has been shown to inhibit colonization by AM fungi [133–136]. Similarly, beneficial effects of epichloid endophytes on the frequency of root colonization by AM fungi have been reported in several wild grasses from Argentina, i.e., *Bromus setifolius* [137] and *Poa bonariensis* [138]. The four-way interactions among grass hosts, epichloid endophytes, AM fungi, and herbivores may alter herbivory and herbivore population dynamics [139]. However, experimental studies researching these interactions are very scarce. Barker [140] found that infection of perennial ryegrass with the AM fungus *Glomus fasciculatum* reduced the antixenotic effect of *E. festucae* var. *lolii* endophyte on Argentine stem weevil, while mycorrhiza had no effect on insect feeding in endophyte-free plants. Vicari et al. [141] evidenced in perennial ryegrass both additive and nonadditive, depending on host P nutrition status, effects of *E. festucae* var. *lolii* endophyte and the mycorrhizal fungus *Glomus mosseae* on growth and survivorship of larvae of the noctuid moth *Phlogophora meticulosa*. The authors suggested that, in terms of insect resistance, the beneficial effect of the epichloid endophyte on perennial ryegrass was reduced by mycorrhizae. The ecological and evolutionary role of the epichloid endophyte/AM mycorrhizal

fungi/host grass species combinations and its implications for the herbivore defense hypothesis merits further research.

Allelopathy. Root exudates can highly affect plant community interactions either indirectly by altering biogeochemical processes within the rhizosphere or directly by inhibiting seed germination or growth of neighboring plants [142,143]. Evidencing the role of shoot-located epichloid endophytes on exudation of phenolic compounds into the rhizosphere by roots of infected grasses was a milestone step in our understanding of endophyte involvement in modification of rhizosphere chemistry resulting effects on plant succession in the ecosystems [24]. Subsequent studies by Guo et al. [144] detected a range of phenolics and other metabolites released by grass roots in response to endophyte presence in the shoots, including sugars, lipids, carboxylic acids. Several of these exudates, i.e., syringic acid (a phenolic compound) and myristic acid (lipid) are known to inhibit germination and growth of monocot and dicot weeds [145,146]. In a study by Renne et al. [147], phenolic-like root exudates from endophyte-infected tall fescue could effectively inhibit germination of a range of native prairie grasses in vitro. However, their effectiveness in inhibiting seed germination in soil was low, suggesting that soil microflora could effectively alter the allelopathic potential of phenolic compounds [148].

Mechanisms of endophyte-induced tolerance to abiotic stresses

Drought stress. Drought stress tolerance of grasses infected with epichloid endophytes has been extensively researched for many decades [23]. Adaptations imparted by the endophytes can be categorized as mechanisms of drought avoidance, tolerance, and recovery from drought [149].

Mechanisms of drought avoidance enable endophyte-infected grasses to maintain an efficient water supply to aboveground organs and conserve water in plant tissues during drought periods. These adaptations include: (i) improved water uptake from the soil by a more extensive root system [37,150–153], (ii) reduced transpiration due to efficient regulation of stomata [37,153–155], and (iii) water storage in plant tissues by accumulation of solutes, likely soluble carbohydrates [155,156].

Drought tolerance adaptations enable plants to withstand periods of short- or long-term water deficit. In endophyte-infected grasses, these adaptations include: (i) accumulation and translocation of assimilates, mainly glucose, fructose, polyols [157], proline [156,158], mannitol, and amino acids [159], (ii) osmotic adjustment to maintain turgor and physiological and biochemical processes [160,161], (iii) maintaining elasticity of cell walls [162,163], and (iv) efficient water use [164,165]. Loline alkaloids, in addition to their function as insecticides, have been shown to lower osmotic potential, thus reducing the effects of drought stress [67]. The enhanced production of antioxidants by endophyte-infected grasses may also be considered as a drought tolerance mechanism to protect meristems and cell membrane functions from detrimental effects of reactive oxygen species (ROS) [27,28,166–168]. Recently, it has been proposed that auxins (or auxin-like compounds) produced by epichloid endophyte hypha in grass host tissues may modulate plant responses to the presence of ROS and prevent cell death [168].

In endophyte-infected grasses drought stress recovery mechanisms include a rapid water uptake by roots and restoration of physiological functions in plant tissues. Beneficial effects on endophyte infection on growth and water relations in tall fescue and meadow fescue were observed during the weeks following drought stress [37,169]. Superior ability of endophyte-infected grasses to regrow quickly after relief from drought has been considered more important for grass persistence than enhanced growth during the period of drought [169].

Dehydrins, a group of proteins synthesized in grasses in response to various abiotic stresses including drought [170], may be also be implicated in endophyte-mediated drought stress tolerance. Dehydrins may play a role in stabilizing hydrophobic interactions and gene transcription [171,172]. In tall fescue, dehydrins were synthesized in endophyte-infected plants earlier during drought stress than in noninfected plants and it was associated with higher tiller survival rate of endophyte-infected plants [173]. Interestingly, endophyte-mediated increase in dehydrin expression was much more

pronounced in mesic than xeric tall fescue types [174], suggesting an additive effect of the endophytes to the already existing mechanisms of drought tolerance in grasses [175].

Our understanding of mechanisms by which endophytes enhance host grass survival during drought is still incomplete. Results suggest that endophyte-mediated responses to water deficit are a combination of drought avoidance, tolerance and recovery mechanisms, and may vary among individual symbionts in the population. Alterations of root architecture [176–178], and morphology and functions [144,179,180] may be the primary basis for drought tolerance in endophyte-infected grasses. Protection of growth meristems and cell membrane functions by antioxidants from oxidative stress caused by excess of free radicals may be a secondary mechanism [27,89,168].

Mineral imbalance stress. Earlier studies evidenced the role of epichloid endophytes and nitrogen fertilization on production of ergot and loline alkaloids [181,182] and metabolites (proline, amino acids) involved in drought stress tolerance [183,184]. Nitrogen effects on grass host growth in response to endophyte infection were inconclusive, depending on grass and endophyte species, and nitrogen availability in the growing medium [23]. However, the majority of those studies indicated that benefits of endophyte infection on herbage growth and plant fitness were expressed under optimal nitrogen fertilization. The endophyte-related mechanism involved in altered nitrogen metabolism of grasses is an increased activity of glutamine synthetase, an enzyme responsible for NH_4^+ reassimilation, regardless of nitrogen availability [182]. Nitrogen metabolism by endophyte in tall fescue appears to involve both assimilatory and basic nitrogen metabolism and may be correlated with mechanisms of in vitro N utilization by endophyte mycelium [182].

A milestone step in our understanding of *E. coenophiala* endophyte involvement in mineral nutrition of grass hosts was the discovery of chemical modifications in the rhizosphere of tall fescue and the regulatory effects root exudates on uptake of certain minerals, i.e., phosphorus (P), aluminum (Al), iron (Fe), and copper (Cu) [179,180,185–187]. Similar responses were later evidenced in perennial ryegrass infected with *E. festucae* var. *lolii* [188]. These root exudates were first characterized as phenolic compounds with antioxidative properties. In subsequent studies, Qawasmeh et al. [28,89] and Guo et al. [144] characterized specific phenolic compounds and other secondary metabolites exuded from roots of tall fescue and perennial ryegrass in response to endophyte infection in shoot tissues. They also found a strong effect of endophyte strains on the quantity and quality of phenolic compounds produced and exuded via roots by grass hosts. At low P availability in soil, exudation of phenolic compounds by roots of endophyte-infected grasses was shown to increase P uptake from nonsoluble P sources, such as phosphate rock [179]. The underlying mechanism of increasing P availability in the soil may be the ability of phenolic compounds to bind (chelate) soluble Al, Fe, and manganese (Mn), which can otherwise render P unavailable [189,190]. In fact, Malinowski and Belesky [186] evidenced an efficient mechanism of Al sequestration on root surfaces of endophyte-infected tall fescue that may increase competitive ability of symbiotic plants grown in acidic soils [191]. Copper chelating properties of phenolic compounds [180] may explain reduced Cu concentrations in endophyte-infected tall fescue forage when compared with noninfected plants [192]. Antioxidative properties of phenolic compounds released into the rhizosphere of endophyte-infected tall fescue were shown to reduce Fe outside of the grass root system [185], a mechanism not known in monocots [193]. This mechanism may contribute to enhanced Fe uptake by endophyte-infected tall fescue [187]. It has been postulated that root exudates may help endophyte-infected grasses by stimulating the activity of soil microbial communities, indirectly enhancing mineral nutrient supply to the host plant [194].

The ability of epichloid endophyte-infected grasses to release root exudates with chelating properties may be used as a method for soil remediation from common metal pollutants, including zinc (Zn) [195,196], Al [186,197], cadmium (Cd) [198,199], and nickel (Ni) [200]. The underlying mechanisms of heavy metal stress tolerance in endophyte-infected grasses may rely on an antioxidant defense system based on phenolic compounds that enhance activities of superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase enzymes to prevent accumulation of H_2O_2 as a result of heavy metal toxicity [199–201]. As a result, endophyte-infected grasses are able to accumulate

greater amounts of heavy metals in shoot tissues than their noninfected counterparts with less damage due to metal toxicity [198]. Studies by Yin et al. [202] have evidenced tolerance of endophyte-infected grasses to saline stress caused by excessive amount of sodium (Na) in nutrient solution, although a mechanism responsible for this phenomenon has not been investigated.

Light stress. Responses of endophyte-infected grasses to light stress are not well understood. Early studies reported lower net photosynthesis (measured in the entire canopy) in response to endophyte infection of tall fescue with increasing light intensity [203]. More efficient competition for light may result in higher biomass productivity of endophyte-infected grasses than their noninfected counterparts when grown in shade, but not in full light [204,205]. Elevated UV-B radiation reduced seed production and increased tiller production in a ryegrass genotype [206]. However, subsequent studies found no interactions between endophyte status and UV-B radiation on morphological parameters in tall fescue, meadow fescue, red fescue (*Festuca rubra*), and perennial ryegrass [207]. Some insects, i.e., desert locust (*Schistocerca gregaria*), may alter feeding preferences for endophyte-free or endophyte-infected leaves of meadow fescue in response to increasing levels of UV-A (320–400 nm) and UV-B (280–320 nm) radiation. Phenolic compounds produced abundantly by endophyte-infected grasses [144,185,208] are known to protect plant tissues from excess UV radiation [209]. This adaptation may explain the prevalence of endophyte-infected grasses with decreasing latitude [210].

Competitive ability of endophyte-infected grasses

The role of antiherbivory metabolites

Environmental conditions and associated biotic and abiotic stress factors define the range of adaptation and production limits of many agronomic and wild grasses. The epichloid endophyte-grass associations have a higher degree of plasticity that contributes to expanded temporal and spatial boundaries of adaptation when compared with noninfected plants [211]. In a competitive environment, grass plant persistence should be improved by epichloid fungal endophytes if herbivores were to inflict more damage on competing noninfected genotypes and plant species that do not harbor endophytes. However, other authors hypothesize that endophyte-induced drought tolerance may be more crucial for competitive ability of grasses than protection from herbivory [212]. Mechanisms of increased tolerance to biotic and abiotic stresses operating in endophyte-infected grasses ultimately lead to improved growth and higher competitive ability when compared with noninfected counterparts and other plant species, in addition to the efficiency of epichloid endophyte transmission between grass host generations [213]. Alkaloids produced by the epichloid endophyte/grass associations are found only within shoot tissues and have not been identified in exudates released from plant roots into the rhizosphere. It is not known if the alkaloids per se might be responsible for below-ground biogeochemical effects associated with endophyte infection, such as allelopathy [214], increased in soil C and N contents in endophyte-infected pastures [215] or alteration of the activity of litter decomposing microorganisms [216,217]. Loline alkaloids, however, have been shown to reduce germination rate of monocot and dicot seeds [218]. Similar allelopathic effects of lolines in soil-grown endophyte-infected tall fescue/competitor associations have been reported by Bush et al. [67] and Malinowski et al. [219]. This suggests that loline alkaloids may have several functions in the grass hosts, including protection from insects, regulation of osmotic potential, and allelopathy. In response to endophyte infection, aqueous extracts from moisture stressed perennial ryegrass pseudostem had allelopathic effects on seedling growth of white clover (*Trifolium repens* L.) [220]. However, the authors excluded the involvement of alkaloids present in the ryegrass genotypes (peramine, ergovaline, and lolitrem B) and suggested an effect of another, not assayed metabolite.

The role of root exudates

The ability to release organic compounds into the rhizosphere, along with improved root and shoot growth and functions, by endophyte-infected grasses may play a very important role not only for mineral acquisition but also intra- and interspecific competitive interactions, and even the structure of soil microbial communities [221–223]. Exudation and composition of root exudates may be highly specific to a particular endophyte/grass genotype association; thus, some endophyte-infected plants may be more competitive than others [144]. Several studies have shown negative effects of endophyte-infected grasses when grown in mixed stands with legumes [219,224,225]. Rutgers et al. [226] observed that plots growing either ‘Kentucky-31’ tall fescue infected with its native endophyte had reduced biomass of other grasses and forbs than plots with ‘Georgia-5’ tall fescue infected with the novel endophyte strain AR542E. Infection of ‘Georgia-5’ tall fescue with its native endophyte strain also resulted in reduced forb biomass when compared to fields growing ‘Georgia-5’ tall fescue infected with the novel endophyte strain AR542 [227]. These results suggest that grasses infected with native endophytes may release different chemicals in the rhizosphere than those release by the novel endophyte/grass combinations. Again, a high variability in growth responses to endophyte infection has been observed among grass species and endophyte strain/grass genotype combinations [228].

Improved grass host growth

In addition to effects on the rhizosphere, epichloid endophytes can alter a range of physiological mechanisms, i.e., photosynthetic rate [203], antioxidant activity [21,28,229], and hormone balance [230,231] in host grasses. At seedling establishment stage, effects of endophyte infection on seedling competitive ability of cultivated and wild grasses have been inconclusive, varying from positive effects on seedling DM and tiller number [232–236] to no effects on these traits [237–239]. Based on results reported by Rudgers et al. [94], it seems that the endophyte may be more important for a successful competition of its grass host during the seedling establishment phase than during the following growth stages. In established plants, numerous morphological traits can be modified by the presence of endophytes, including heavier and more numerous tillers [240], greater leaf elongation rate [37,241], and altered root architecture [242]. These adaptations can ultimately result in a superior growth and persistence of endophyte-infected grasses when compared with noninfected plants under a range of environmental constrains [23,243]. In time, endophyte-infected grasses can dominate plant communities, thus reducing plant diversity in successional fields [41]. An interesting question raised by Chen et al. [244] was how elevated CO₂ concentrations that are expected to increase from the current 390 ppm to around 1,000 ppm by 2100 [245] would affect known endophyte effects on grass hosts. Except for results presented by Marks and Clay [228] and Hunt et al. [246], other studies evidenced negative effects of endophytes on growth, physiological and biochemical parameters at elevated CO₂ concentrations when compared with these at ambient CO₂ level [52,244,247]. The benefits of endophyte infection for competitive ability of their grass hosts, therefore, may be reduced if the CO₂ concentrations in the atmosphere continue to increase.

Epichloid endophytes in summer-dormant cool-season grasses

There is very limited information on epichloid endophyte effects on competitive ability of summer-dormant tall fescue. Summer dormancy is an endogenous adaptive mechanism developed in some cool-season perennial grasses originating from Mediterranean environments to survive the period of prolonged and severe summer drought [248]. Although endophyte infection rates are usually high among Mediterranean tall fescue accessions [249–251], endophyte benefits to summer-dormant tall fescue in terms of superior tolerance to drought stress when compared noninfected plants are none or negligible [13,251]. It is likely because these tall fescue morphotypes already possess a very efficient endogenous mechanism of summer dormancy (which in fact is a drought

avoidance mechanism) which protects the plants from summer drought [24,252]. Similarly to continental tall fescue, roots of endophyte-infected summer-dormant tall fescue release phenolic compounds with antioxidant activity, thus may give advantage to summer-dormant fescue exposed to mineral imbalance stress in the soil [180]. In a study by Malinowski et al. [253], neither native nor novel endophyte strains had any effect on competitive ability of summer-dormant tall fescue grown in binary mixtures with alfalfa (*Medicago sativa* L.), regardless of soil moisture supply during summer. In contrast, endophyte-infected temperate tall fescue had higher competitive ability than noninfected plants, but only under nonlimiting soil moisture conditions.

Epichloid endophytes in nonagronomic grasses

In Arizona fescue (*F. arizonica* Vasey) infection with *Neotyphodium starrii* (J. F. White & Morgan-Jones) Glenn, C. W. Bacon & Hanlin, a nonepichloid endophyte [5] does not seem to confer any competitive advantages of symbiotic plants or it may even be detrimental to grass hosts [237]. A similar parasitic effect on competitive ability was reported for *Bromus sylvaticus* (Huds.) Pollich infected with *E. sylvatica* endophyte [254]. In their meta-analysis of endophyte effects on grass competitiveness, Saikkonen et al. [255] suggested that endophyte effects on grass host competitive ability may differ in genetically homogenous, agronomic grasses from these observed in genetically highly variable, wild grass–endophyte populations and communities. Additive effects of high genotypic variation in the endophyte strains and grass host genotypes may further magnify the variable outcomes of endophyte infection on competitive ability of grasses at the plant community level [139].

Human-made endophyte–grass associations

Competitive advantages of epichloid endophyte/grass associations resulted in selection of novel endophyte strains that produce marginal amounts or no alkaloids detrimental to grazing livestock, yet retain grass host tolerance to abiotic and biotic stresses [256,257]. These so-called novel endophytes are endophyte strains selected from native endophyte-infected grass accessions that have known and understood alkaloid profiles both when grown in *in vitro* cultures and in associations with their grass hosts. The lack of detrimental effects on grazing animals, as the primary selection criterion, has been proven very successful in numerous studies evaluating a range of novel endophyte strains [257–262]. Gundel et al. [263] have adopted the term “symbiotically modified organisms” or SMO to accommodate the new technology of human-made novel endophyte-grass associations. The technology has resulted in a release of several cultivars of tall fescue and perennial ryegrass, i.e., ‘Jesup MaxQ’ and ‘Georgia 5 MaxQ’ tall fescue reinfected with the novel endophyte strain AR542 [264], ‘HiMag’ tall fescue reinfected with endophyte strain UA4 [260], ‘Texoma MaxQ II’ tall fescue reinfected with endophyte strain AR584 [265], perennial ryegrass cultivars ‘Bealey’, ‘Rohan’, ‘Trojan’ reinfected with the endophyte strain NEA2, ‘Shogun’ reinfected with endophyte strain NEA, ‘Alto’ and ‘Arrow’ reinfected with endophyte strain AR1, ‘Alto’ and ‘Governor’ reinfected with endophyte strain AR37 [266], and ‘Viscount’ ryegrass reinfected with endophyte strain NEA and ‘Impact 2’ reinfected with the endophyte strain NEA2 [267].

The effects of novel endophytes on their grass host resistance to invertebrate herbivory, nematodes, and plant pathogen stresses are inconclusive. In some novel endophyte-grass host associations, insect herbivory has been reduced in a similar way as that in grasses infected with native endophytes [268]. In contrast, other studies evidenced detrimental effects of novel endophytes when compared to grasses infected with native endophyte strains on insect herbivory [86,269,270] or nematode infestation [271]. It is suggested that novel endophytes may often benefit their grass hosts in a similar way to native endophytes in terms of greater tolerance to abiotic stresses that observed in noninfected plants [24]. In contrast to continental tall fescue, responses of Mediterranean tall fescue morphotypes to infection with novel endophytes are manifested to

much lesser extent, especially in terms of drought stress tolerance, likely because of an overlapping endogenous mechanism of drought avoidance [24,272].

Gundel et al. [263] have presented an excellent meta-analysis of the literature comparing effects of novel epichloid endophytes with those of native epichloid endophytes and endophyte-free grasses on many aspects of biotic and abiotic stress tolerance previously described in grasses infected with native endophytes. Overall, animals preferred grasses infected with novel endophytes or noninfected over grasses infected with native endophytes, which also is reflected in their weight gains and performance. Grasses infected with novel endophytes produced similar forage yield to grasses infected with native endophytes and higher than noninfected grasses. However, the number of studies was too small to detect any significant benefits of the reinfection of grasses with novel endophytes on root biomass and tillering. Novel endophytes do not produce alkaloids detrimental to animal performance; however, there is a trend of generally lower production of other alkaloids by grasses infected with novel endophytes when compared to grasses infected with native endophytes. Despite that, neither below- or aboveground herbivory by invertebrates was affected by novel endophytes. Competitive ability of grasses infected with novel endophytes, especially tall fescue, was greater than that of grasses infected with native endophytes. However, detailed analysis of the competitive advantages of novel endophyte–grass associations has not been presented. The authors suggest that, based on the published data, the associations between host grass cultivars and novel endophytes are stable, both in terms of endophyte biomass in plants and infection frequency in plant populations. However, Ju et al. [273] evidenced temperature as major environmental factor affecting colonization of tall fescue tillers, and in consequence transmission of novel endophytes via seeds.

Conclusions

Epichloë sp. endophytes have evolved with their Pooid grass hosts forming associations ranging from antagonistic to mutualistic. The mutualistic epichloid endophytes benefit their grass hosts by helping them to tolerate various biotic and abiotic stresses, ultimately increasing the dominance of symbiotic grass plants in and beyond their native ecosystems. Most of our knowledge on the beneficial effects of epichloid endophyte infection is based on results from agronomic studies with a few important forage grasses, i.e., tall fescue, meadow fescue, and perennial ryegrass, and turf grasses (fescues) that usually were not endemic in the experimental areas. In much more heterogenic populations of wild grasses, the benefits of endophyte infection may often be confounded by underlying genetic variability of the host grasses and their endophyte strains. Epichloid endophytes have been shown to affect multiple functions of the ecosystems and multiple trophic levels, i.e., carbon flow, soil microbial activity, the structure of soil aggregates, soil water dynamics, and flora and fauna community structures. Ultimately, the mutualistic endophytes may increase the competitive ability of their grass hosts by affecting plant growth rate, size, reproductive capacity, and tolerance to environmental stresses. Future research on epichloid endophyte–grass symbioses should focus on adaptations to rapid changes in climatic patterns observed worldwide in the past two decades, especially in regard to increasing concentrations of CO₂ and temperature and decreasing precipitation in the southern latitudes. These environments, dominated by warm-season vegetation, have already been considered marginal for symbiotic cool-season grasses.

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***Epichloë* (dawniej *Neotyphodium*) grzybowe endofity zwiększają adaptacje traw zimotrwałych do stresów środowiskowych**

Streszczenie

W trakcie ewolucji, wiele gatunków traw zimotrwałych ukształtowało symbiozy z bezpłciowymi, bezobjawowymi grzybowymi endofytami z rodzaju *Epichloë* (dawniej *Neotyphodium*) z rodziny Clavicipitaceae. Zależności pomiędzy tymi organizmami obejmują zarówno relacje pasożytnicze jak i mutualistyczne, i mają ogromny wpływ na szlaki metaboliczne traw, np. zwiększają odporność na wiele stresów środowiskowych (susza, zaburzenia równowagi mineralnej w glebie) i biotycznych (uszkodzenia liści przez zwierzęta kręgowo i bezkręgowo, pasożytnicze nicienie, patogeny i konkurencję z innymi roślinami). Niektóre szczepy endofytów wytwarzają szereg alkaloidów i innych wtórnych związków chemicznych, które mogą mieć szkodliwy wpływ na zwierzęta wypasane na symbiotycznych trawach. W ciągu ostatnich dwóch dekad zostały wyizolowane szczepy endofytów, które nie produkują związków chemicznych szkodliwych dla zwierząt, tj. alkaloidy z grupy ergot czy lolitrem. Te nowe szczepy endofitów zostały wprowadzone do kilku odmian traw pastwiskowych z myślą o zwiększeniu ich odporności na stresy środowiskowe, ale bez negatywnego wpływu na wypasane zwierzęta hodowlane w celu zapewnienia wysokiej zdolności konkurencji symbiotycznych odmian traw z chwastami. W niniejszej pracy omawiamy mechanizmy odpowiedzialne za większą zdolność konkurencyjną symbiotycznych traw oraz konsekwencje tej symbiozy dla ekosystemów roślinnych.